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OENOTHERA RUBRINERVIS, A HALF MUTANT

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In the spring of 1913 in a culture of *Oenothera rubrinervis* I noticed some young plants, the leaves of which were a little broader than those of the other rosettes. Although the difference was very small, I planted them separately and saw that the deviation did not increase until the time of flowering. The spikes, however, gave proof that the aberrant specimens constituted a type of their own, since the bracts repeated the marks of the primordial leaves, being broader and more flattened than in ordinary *rubrinervis*. There were 7 specimens of the new form among a culture of 25 plants, all of which flowered in August. This indicates a percentage of about 30. In the following year the seeds of the new form gave a uniform progeny, whereas those of the normal specimens repeated the splitting. Thereupon I studied their seeds and found that about one-fourth of those of *O. rubrinervis* were empty, but almost every seed of the new type contained a living embryo. On account of this very small but constant difference the new form was designated as mut. *deserens*.[1] Evidently it might have escaped observation in previous years, the individuals simply being taken for weaker specimens of the type. I studied the progeny of as many self-fertilized specimens of *O. rubrinervis* as were available, therefore, and found the new type among all of them, and as a rule in correspondingly high numbers. Different strains of *rubrinervis* yielded the same result.

[1] Zeitschr. f. Ind. Abst. **16**: 262. 1916.

If we should apply the principle of BARTLETT concerning mass mutation, and that of MORGAN concerning lethal factors to this case, as I have made use of them in explaining the secondary mutability of *O. grandiflora* and *O. Lamarckiana*,[2] we would conclude that *O. deserens* is a mass mutation of *O. rubrinervis*, and as such is a repetition of the initial mutation which produced the *O. rubrinervis* from *O. Lamarckiana* in my garden. This initial mutation must have occurred in a sexual cell, which, after copulation with a normal gamete of *O. Lamarckiana*, gave rise to a half mutant, *O. rubrinervis*. In other words, *O. rubrinervis* arose as a half mutant between potential *O. deserens* and normal *O. Lamarckiana*. This half mutant, after artificial self-fertilization, must have produced a splitting into three types, exactly in the same way as this splitting can be observed in the half mutants of *O. gigas nanella*. Of these types two must be constant, but the third must repeat the splitting. *O. deserens* is one of the constant ones, whereas the other is assumed to be hidden in the empty seeds, containing a lethal factor just as in *O. grandiflora* and *O. Lamarckiana*. The third type is the continuance of *O. rubrinervis*, and repeats the splitting in every generation.

According to my view *O. Lamarckiana* produces yearly two kinds of gametes in consequence of a secondary mutability into *velutina*. These *velutina* are linked to a lethal factor, which kills them in the young seeds. If we assume that the mutation into *deserens* took place in the typical gametes, leaving the *velutina* unchanged, we would conclude that *O. rubrinervis* consists of two types of gametes, even as *O. Lamarckiana*, but that both of them are in a mutated condition. One is the new *deserens*, without lethal factor; the other is the old *velutina*, linked to a lethal factor. The result of self-fertilization is now easily explained; the copulation of *deserens* gametes among themselves must produce this form, that of *velutina* must give empty seeds, and the combination of the two types must repeat the *rubrinervis* with its splitting capacity.

On the same basis the occurrence of twin hybrids may be explained, the *deserens* gametes giving the *laeta* hybrids; but here we have a considerable advantage over other instances of twin

[2] Mass mutation and twin hybrids of *Oenothera grandiflora* Ait. BOT. GAZ. 65: 377–422. 1918.

hybrids, since both the constituents are available in pure condition for controlling crosses. Any cross which gives twins with *rubrinervis* may be repeated with *O. deserens* and with my *O.* mut. *velutina* (*O. blandina*). In the first case the result must be hybrids of the type *laeta*, in the second case hybrids of the form *velutina*, and the addition of these must simply duplicate the split progeny of the corresponding cross of *O. rubrinervis*. I have made these crosses in a number of cases and found this deduction verified.

Apart from the described secondary mutability into viable *deserens* and dead *velutina* germs, *O. rubrinervis* is not known to possess any noticeable degree of mutability; it has, especially, never produced those mutants which are of so common occurrence in allied mutating forms. Thus we see that secondary mutability is not, in itself, to be considered as a cause of further mutations, and this seems to me to be a fact of paramount interest in the discussion concerning the probable causes of this phenomenon.

The details of the following experiments will give proof of the proposed conception. I shall first give those relating to self-fertilizations and afterward deal with the crosses.

Oenothera rubrinervis originated in my garden from *O. Lamarckiana* quite regularly in a percentage of about 0.1. Every time the visible characters were exactly the same. Between 1890 and 1900 the mutation was repeated 66 times among 66,000 plants.[3] In 1905 I introduced new rosettes of *O. Lamarckiana* from the original locality near Hilversum into my garden, and among their offspring I observed also repeated mutations into *rubrinervis*. The characters were always the same, namely, a pale reddish tinge, narrow and longitudinally folded leaves, a hairy epidermis, cup-shaped flowers, but above all the brittleness of the stems, branches, and petioles, due to the incomplete development of the cell walls in the fibers of the bark and wood. Until now I cultivated mainly two strains, derived from two different mutants of 1895. One of them has given the material for all my crosses, and I shall designate it as the main line. The second line of 1895 was originally destined for control experiments only, but in 1913 it produced the first observed

[3] The mutation theory, English ed. 1:331. 1909.

case of *O. deserens*, as previously mentioned, and since then it has been studied carefully in this respect.

After repeated cultures of pure *O. deserens* had been made and compared with *O. rubrinervis*, the characteristic marks of the two forms became quite clear and reliable, although very small. In mixed cultures the types may even be separated when very young, but some dubious specimens may remain. At the time of flowering these have almost always been shown to belong to the new type. Among the very young rosettes, with only 3–5 leaves, those of *deserens* are broader and more flattened and of a deeper and purer green, resembling therein young plants of *O. Lamarckiana*. These differences increase slowly until the time when the rosettes must be planted out from the boxes into the garden, about the middle of April. The leaves of *O. deserens* have now a broader base and a less pointed top than those of *O. rubrinervis*, besides the marks already given. In July the differences remain very small, the two types reaching the same height at the same period, but the *rubrinervis* begin to flower one or two weeks earlier than the *deserens*. Seen from above, the spikes show narrow, folded bracts in the first type and flat, broad ones in the second type. This character is easily appreciated and wholly reliable; no dubious cases trouble the counting in mixed cultures. The beginning of August, when the *deserens* have opened only a few of their first flowers, is the best time to separate them. A difference in the color has now become clear, the red tinge of the parent type failing in the *deserens*. Here the leaves, bracts, and flower buds are green, and the flowers are also of a purer yellow. A number of smaller marks, which are helpful in the distinction, almost escape description, as, for example, the form of the flowers, their grouping at the top of the spike, and the more erect position of the buds before opening.

The main character of *O. rubrinervis* is the brittleness of all its parts, as already mentioned. It is exactly the same in *O. deserens*. I have broken the stems of all the plants to be mentioned in this article at the time of sorting them out in August or after harvesting their seeds, but no exception has been found to this rule.[4] Hybrids

[4] I have, moreover, injected all the seeds for the sowings of the later years under a pressure of 8 atmospheres during 48 hours, this being the only reliable means of making the germination as complete as possible.

which possess the other characters of *rubrinervis*, but lack the brittleness, are easily recognizable as rosettes of radical leaves as well as during the growth of the stems. They will be designated as *subrobusta*.[5]

The determination of the percentage of mutants in self-fertilized seeds was made in 1916 in the following manner. The specimens were counted in the boxes at the time of planting out in April and the most undoubtful specimens of *rubrinervis* were counted and destroyed. All the others were planted out and tried at the time of flowering in August. By this means the space required for the cultures was reduced to about one-half of what would have been necessary if all the plants had been set out. Some losses were unavoidable and the percentage figures may be a little too small in ordinary cases. Only under favorable conditions do they come up to the amount of the theoretical expectation, namely, one-third of all the individuals. Since my question, however, was mainly to decide whether all specimens of *rubrinervis* split into this form and *deserens*, or whether there are also plants with a uniform progeny, I shall give the figures as I found them.

PERCENTAGE OF *O. deserens* AMONG CULTURES OF *O. rubrinervis*

Seeds of	Parent number	Number of specimens	Percentage of *deserens*	Mean
Third generation in 1910....	1	60	10	
1913....	2	59	20	
1913....	3	60	22	
1914....	4	59	19	19
1914....	5	60	25	
1914....	6	59	19	
1914....	7	60	15	
Fourth generation in 1915....	1	89	16	
1915....	2	60	25	18
1915....	3	79	13	
1915....	4	89	19	

In the first place, I shall now describe the main line of *O. rubrinervis*. Part of the seeds of the original mutant of 1895 had been preserved until 1905; they germinated sufficiently and gave the second generation. From this a third generation was derived in 1910, 1913, and 1914, and a fourth in 1913, 1914, and 1915. All the parents of these generations have been artificially fertilized by

[5] Gruppenweise Artbildung, p. 143. 1913.

myself. In 1914 I observed for the first time a specimen of *deserens* among these cultures, and this in a third generation. Thereupon I sowed in 1916 the self-fertilized seeds of 11 specimens in order to decide whether all of them would repeat the splitting and to determine roughly the percentage of the new type. The results are given on page 5. From these figures we see that all the specimens tried show the same splitting, and that this is always a mass mutation.

The countings for this table were partly made in the stadium of the young rosettes and partly at the time of flowering. In order to prove the correctness of this process, I repeated the sowings in 1917 for those of the parents of which sufficient seed had been preserved, planted out all of their seedlings, and counted them in August, when they were ripening their first fruits. The results are as follows:

Seeds of		Parent number	Number of specimens	Percentage of *deserens*	Mean
Third generation in	1913....	2	48	15	16
	1914....	4	55	24	
	1914....	6	59	13	
	1914....	7	53	13	
Fourth generation in	1915....	1	58	14	
	1915....	4	57	19	

Although the cultures were but small, they show that the deviations from the theoretically expected result (25 per cent) do not depend upon the method of counting as used in 1916.

In this race I self-fertilized the first mutant *deserens* observed in 1914 and derived from it a second and a third generation in 1915 and 1916. The second generation consisted of 95 plants, of which 50 flowered; the third was derived from two parents and embraced 77 and 140 specimens, among which 60 and 60 were left to flower. All of these cultures were wholly uniform at the time of planting out as well as during the flowering period. No *rubrinervis* and no new mutants occurred among them. Thus *O. deserens* is seen to constitute a pure and uniform race.

The percentage of empty grains among the seeds has been given elsewhere for this race of *O. rubrinervis*.[6] The determination was made in the harvest of 5 plants of the third generation grown in

[6] Zeitschr. f. Ind. Abst. **16**: 262. 1916.

1910 and 1915, and in that of two specimens of the fourth generation of 1915. I found 53–68 per cent of germs, with a mean of 60 per cent. Among the specimens of *deserens*, quoted in the same table, 5 belonged to this race; their seeds contained 96, 99, 94, 83, and 58 per cent of good germs. Thus we see that the empty grains, which are a character of *O. rubrinervis*, have disappeared almost wholly in the new mutant.

My second strain of *O. rubrinervis* was derived from another mutant of 1895. It has not been used for any crosses except those mentioned in this article, and which served as control for the experiments in the main line. Part of the seeds of 1895 were sowed in 1907 and yielded a second generation from which a third has been derived in 1913 and a fourth in 1914. I counted the *deserens* for three parent plants as previously described and found the percentages as follows:

PERCENTAGE OF *O. deserens* IN CULTURES OF *O. rubrinervis*

Seeds of	Culture	Number of specimens	Percentage of *deserens*	Mean
Second generation in 1910....	1913	25	28	19
Third generation in 1913....	1914 (A)	70	14	
Third generation in 1913....	1914 (B)	70	16	

The results agree exactly with those deduced from the previous table. The suspicion, however, that in the two last cases the percentage figures were found too low, on account of losses of specimens of *deserens* at the time of planting out, induced me to repeat these sowings in 1916 from preserved seeds, giving them all the care which the previous cultures and the first ones of 1916 had shown to be necessary. Moreover, in 1913 I had self-fertilized a third plant, besides the two mentioned in the table, and also sowed its seeds. In this way I got in 1916 the following percentages for the seeds of the three self-fertilized plants of 1913:

PERCENTAGES OF *O. deserens* IN CULTURES OF *O. rubrinervis*, STRAIN B

Seeds of third generation	Number of specimens	Number of *deserens*	Percentage of *deserens*	Mean
Plant A.....	84	32	38	30
B.....	90	25	28	
C.....	98	22	25	

The result confirms the expectation and shows that the figures given in the former table, although they give proof of the occurrence of mass mutation among the offspring of every plant of *rubrinervis*, are too low for the appreciation of the exact percentage of *deserens*. This must be estimated at about 30 per cent, or almost one-third of the whole progeny. In this race I self-fertilized three mutants in 1913 and two specimens of *deserens* among their offspring in 1915. I cultivated 150+84+180 specimens of the first group and left about one-half of them to flower, and 70+89 plants of the second group, all of which flowered in 1916. I had 573 plants in all, among which 319 bore flowers and fruits. They were all uniformly *deserens*, showing the marks of the type as previously described. No specimens of *rubrinervis* and no new mutants were observed among them. For one mutant of 1913 and for two plants of the second generation in 1915 I determined the amount of germs in the seeds and found 97–96 and 98 per cent, or an almost total absence of empty grains.

Besides the two described families of *O. rubrinervis* I have controlled the seeds of some mutants in order to know whether all of them contained specimens of *O. deserens* and in percentages pointing to mass mutation. I found the following figures:

PERCENTAGE OF *deserens* AMONG THE OFFSPRING OF MUTANTS

Mutant *rubrinervis* from	Number of offspring	Percentage of *deserens*
O. Lamarckiana, 1910.....	25	12
O. Lamarckiana, 1910.....	60	15
O. pallescens, 1911.....	25	16

The strain of *O. Lamarckiana* was derived from a rosette found in the original station near Hilversum in 1905, and the *pallescens* had been a mutant from this same strain.[7] Although the cultures were small, they prove the existence of mass mutation. I sowed the seeds of a specimen of *deserens* from the first culture in 1914, cultivated 25 flowering plants, and found these uniform with the type of their parent.

[7] New dimorphic mutants of the Oenotheras. BOT. GAZ. **62**:262. 1916.

Summing up the results of all the tables, we may conclude that all specimens of *O. rubrinervis*, derived from various sources, and the mutants as well as their offspring, show mass mutation into *O. deserens*, besides a considerable number of empty seeds. Taking into consideration the unavoidable losses in the numerical estimations, we may further conclude that *O. rubrinervis* produces about one-fourth empty seeds, and among the living offspring about one-third *O. deserens*, which are constant in their progeny and have no empty grains, or almost none. This points to a relation of 1:2:1 for the whole harvest. The phenomenon is thus shown to be parallel to the splitting of the hybrid mutant of *O. gigas nanella* and to the mass mutability of *O. grandiflora* and of *O. Lamarckiana* itself.

CROSSES BETWEEN O. RUBRINERVIS AND O. DESERENS.—If this explanation is true, it may be confirmed by means of crossing *O. rubrinervis* with its mass mutant. The sexual cells of the first are about one-half *deserens* without a lethal factor, and the rest *velutina* provided with such a factor; those of *O. deserens*, however, are uniformly so. We must expect, therefore, a splitting into almost equal parts of *deserens*×*deserens*=*O. deserens*, and of *velutina*×*deserens*=*O. rubrinervis*. I made both the reciprocal crosses in 1915, cultivated 58 and 50 specimens of their offspring in 1916, and counted them at the beginning of the flowering period in July, finding as follows:

	Percentage of *rubrinervis*	Percentage of *deserens*
O. rubrinervis×O. deserens..	48	52
O. deserens×O. rubrinervis..	78	22

The two types of hybrids resembled their parents exactly, and the figures point to numerical equality of the two groups, although the cultures were only small. Thus we see that the expectation from our formula is confirmed by the experiment.

TWIN HYBRIDS OF O. RUBRINERVIS.—The twin hybrids of *O. Lamarckiana* and *O. grandiflora* are now explained as the result of the mass mutation of these species, but the experimental proof is not complete as yet because neither of these species is known to occur without that form of mutation. In this respect the case of

O. rubrinervis is far stronger, since its two constituents are both represented in my cultures. This fact makes a complete analysis possible, as I have already pointed out. If *O. rubrinervis* is split by some cross into *laeta* and *velutina* on account of its composition of gametes of *deserens* and *velutina*, then the corresponding cross with *O. deserens* must evidently give the same *laeta* and that with *O. Lamarckiana* mut. *velutina* the same *velutina*. Thus the split progeny can be duplicated by the addition of its components.

I have described the splitting crosses in *Gruppenweise Artbildung* (pp. 122, 196–200, 1913) and repeated some of them so as to have the dimorphic progeny together with the cultures of the presumed constituents, in order to be able to identify their characters during the whole time of their development. The percentage figures given in my book are as follows:

TWIN HYBRIDS OF *O. rubrinervis*

Cross	Percentage of *laeta*	Percentage of *velutina*
O. biennis×rubrinervis	30–49	51–70
O. rubrinervis×O. biennis Chicago	39–44	56–61
O. rubrinervis×O. Cockerelli	49	51
Mean	42	58

In the second and third generation of the two latter crosses the *laeta* have split off brittle *rubrinervis* in about one-third of the cultures, whereas the *velutina* remained constant.

I repeated the two first named crosses in 1915, but not the third one. On the other hand, I have repeated the cross with *O. Hookeri*, in the progeny of which I had previously not been able to distinguish the twin types. I had the following cultures in 1916. Most of these plants flowered in August.

TWIN HYBRIDS OF *O. rubrinervis;* CULTURES OF 1916

Cross	Number of specimens	Percentage of *laeta*	Percentage of *velutina*
O. biennis×rubrinervis	59	46	54
O. rubrinervis×O. biennis Chicago	60	53	47
O. Hookeri×rubrinervis	60	20	80
Mean	.....	40	60

The results coincide with the previous ones as nearly as might be expected. The types of the twins were the same as those in the older cultures.

For these twins I have determined the amount of empty grains, self-fertilizing two specimens of each of them in August 1916 and counting out 100 seeds for each parent.

PERCENTAGE OF GERMS IN SEEDS OF *laeta* AND *velutina*

Cross	Parent number	*laeta*	*velutina*
O. biennis×rubrinervis	1	93	3
	2	96	4
O. rubrinervis×Chicago	1	94	28
	2	95	31
O. Hookeri×rubrinervis	1	94	59
	2	95	71

As in other cases, the seeds of the *laeta* hardly contain any empty grains, whereas those of the *velutina* are often badly developed.

My task was now to repeat these crosses, substituting *O.* mut. *deserens* and *O.* mut. *velutina* for *O. rubrinervis*. The latter group of crosses have already been described elsewhere;[8] they yielded pure cultures of *velutina* which in every case were exactly like the *velutina* of the corresponding cross with *O. Lamarckiana*. The crosses with *O. deserens* were made in 1915 and their progeny studied in 1916; it was in every case wholly uniform.

CROSSES OF *O.* MUT. *deserens*

Cross	Number of specimens	Type
O. biennis×deserens	60	O. (bien.×Lam.) laeta
O. syrticola×deserens	70	O. (syrtic.×Lam.) laeta
O. Hookeri×deserens	60	O. (Hook.×Lam.) laeta
O. deserens×biennis Chicago	70	O. (Lam.×Chic.) laeta

About one-half of each culture flowered and developed their fruits. For each culture a control parcel was cultivated with the *laeta* from the corresponding cross with *O. Lamarckiana*, and they were compared during all the time of their development. I could

[8] Kreuzungen von *Oenothera Lamarckiana* mut. *velutina*. Zeitschr. f. Ind. Abst. 17:1917.

not find any differences. The descriptions for the *deserens laeta* are exactly the same as those given previously for the *Lamarckiana laeta*. Although I have not made the cross *O. syrticola*×*O. rubrinervis*, I have added the second experiment of the table. From this and the result of *O. syrticola*×*O. blandina* (mut. *velutina*) described in my former article the result of the cross *O. syrticola*× *rubrinervis* may be predicted, and so it would be in other cases also.

Summing up the results of these experiments, we see that in producing twin hybrids *O. rubrinervis* is split in exactly the same way as an artificial mixture of about equal parts of gametes of *O. deserens* and *O.* mut. *velutina* would be. The conclusion that its gametes really possess this dimorphy is thereby as clearly proven as might be expected.

CROSSES OF O. RUBRINERVIS WITH O. LAMARCKIANA AND ITS DERIVATIVES.—In *Gruppenweise Artbildung* I have described the first generation of these crosses as consisting of two types, *O. Lamarckiana* and *O.* hybr. *subrobusta*. The latter is a *rubrinervis* in which the brittleness fails, and thereby very similar to our new mut. *erythrina*;[9] but this similarity is only an external one, since after self-fertilization the hybrid *subrobusta* splits off, as a rule, brittle *rubrinervis* plants, whereas the *erythrina* produces the *decipiens*, which is not brittle. Shortly after publishing my book, however, I discovered in the summer of 1913, among the progeny of a cross of *O. rubrinervis* and *O. Lamarckiana*, a slight difference among the *Lamarckiana*-like plants. Some of them were stouter and had broader and less crinkled leaves than the others. I self-fertilized them and got a culture, which, although not uniform, repeated the deviating marks of the parental type in the majority of the individuals. I shall call this hybrid type *lucida*. Moreover, in making a large number of crosses of individuals of the same family of *rubrinervis* with *Lamarckiana* plants from various sources, as well as different mutant strains, I discovered that the second hybrid type is not always the solid *subrobusta*, but sometimes the brittle *rubrinervis*. I have not as yet discovered why this should be so. We should expect the brittleness to be recessive to the production of

[9] Zeitschr. f. Ind. Abst. **16**:262. 1916.

strong fibers, and as a rule it is so, but not always. The two contrasting cases have occurred mainly in strains derived from different initial plants, and some hidden mutation might be responsible for the dominance of the brittleness. This seems to be the case at least in *O. nanella*, but the number of crosses in each of my different families of dwarfs is too small to decide whether this is the real cause. Crosses of *O. rubrinervis* with other mutants than the dwarfs have also given sometimes the brittle form and sometimes the *subrobusta* for the second hybrid.

If we keep in mind that the hybrid *rubrinervis* is only a brittle form of the hybrid *subrobusta*, and that the one may be substituted for the other for unknown reasons, the following descriptions will easily be understood. I might add, however, that from a single cross between two individual parents both types never arise simultaneously in the first generation. In the succeeding generations the *rubrinervis* as a rule are constant, whereas the *subrobusta* may split off the brittle form.

If we assume the gametes of *O. Lamarckiana* to consist of equal parts of typical ones and of *velutina*, and those of *O. rubrinervis* to consist of *deserens* and *velutina*, *O. Lamarckiana*×*O. rubrinervis* must yield 25 per cent *typica*×*deserens*, 25 per cent *typica*×*velutina*, 25 per cent *velutina*×*deserens*, and 25 per cent *velutina*×*velutina*. The last combination will produce empty grains, since the same lethal factor comes in from both sides; on the other hand, the three first named combinations must give viable seeds. *Typica*×*velutina* is the formula for *O. Lamarckiana*, and *velutina*×*deserens* that for *O. rubrinervis* and *subrobusta*, and so the occurrence of these hybrid types is easily explained. The remaining combination *typica*×*deserens* must then be assumed to give the new hybrid *lucida*, and this can be verified by crossing *O. deserens* with *O. Lamarckiana*. All these deductions are, of course, the same for the reciprocal crosses. If these deductions are reliable, they show that the polymorphy of the first generation of hybrids between the two older forms is due to the combination of their capacities to produce twins in other crosses. In other words, it is a natural sequence of their secondary mutability. I shall now describe the experiments which seem to me to justify these deductions.

O. LAMARCKIANA×O. RUBRINERVIS.—According to the deductions just given the expectation for this cross is

O. Lamarckiana×*O. rubrinervis* =
(typica+velutina)×(deserens+velutina) =
typ.×des.+vel.×des.+typ.×vel.+vel.×vel. =
lucida subrobusta Lamarckiana empty grains
or
rubrinervis

In the first place, I determined the amount of empty grains, using the same method as in previous cases.

Cross	Parent number	Cross	Percentage of germs
O. Lamarckiana×rubrinervis.....	1	1913	21
	2		29
	3		33
O. rubrinervis×Lamarckiana.....	1	1913	48
	2		60

The presence of empty grains is thereby proven, although the percentages of germs are much smaller than would be expected; but this may be due to quite different causes, as has been shown elsewhere.

In the second place, I studied the living progeny for the fourth cross of this table and for a cross made in 1907 with another strain of *O. Lamarckiana*. Each of these cultures was trimorphous, containing the types *Lamarckiana* and *lucida*, and besides these either *subrobusta* or *rubrinervis* (that is, tough or brittle).

Cross	Number of Specimens	Percentage of		
		Lamarckiana	*lucida*	*subrobusta* or *rubrinervis*
O. rubrinervis×Lamarckiana 1913	60	32	20	48 rubrinervis
1907	69	40	6	54 subrobusta
Mean.....	.....	36	13	51

The expectation would be for equal parts, but for some unknown reason the *lucida* almost always fall short of this. Apart from this difficulty the results of these cultures coincide with the theoretical

deductions from our formula. I have made quite a number of further crosses between these two forms, partly in 1905 and partly in 1913, using always the same family of *rubrinervis*, and taking the combinations in both reciprocal directions. Six of them have given for the third hybrid type *rubrinervis* and three of them *subrobusta;* but since I have not determined the amount of *lucida* among them, it is of no use to give the percentage figures.

The exactness of the identification of the types in the formula can be controlled by direct crosses with the constituents mut. *deserens* and mut. *velutina*. The latter has been described under the synonym *O. blandina*. I made the following combinations:

Cross	Year	Number of plants	Percentage of		
			lucida	*subrobusta*	*velutina*
O. deserens×Lamarckiana	1915	49	18	82	0
O. rubrinervis×blandina	1915	70	0	50	50
O. blandina×rubrinervis	1913	70	0	53	47
O. deserens×blandina	1915	70	0	100	0
O. blandina×deserens	1915	49	0	100	0

The expectation for these crosses was:

O. deserens×Lamarckiana = O. deserens×(typ.+velutina) = lucida+subrobusta
O. blandina×rubrinervis = O. blandina×(deserens+velutina) = subrobusta+velutina
O. blandina×deserens = O. blandina×(deserens) = subrobusta

Apart from the figure for *lucida*, which is too small, the results of the experiments directly confirm the expectation. I have determined the amount of empty seeds for the four last named crosses, and found almost none:

Cross	Percentage of germs in seeds
O. rubrinervis×blandina	97
O. blandina×rubrinervis	91
O. deserens×blandina	100
O. blandina×deserens	90

Moreover, I made the same determinations for the hybrids from the two first named of these crosses, self-fertilizing them in 1916. For the two latter crosses it was evident that the hybrids would

hardly have any empty grains, and I did not think it necessary to control this.

Cross	Parent number	Percentage of germs in seeds of	
		subrobusta	*velutina*
O. rubrinervis×blandina	1	96	70
	2	97	75
	3	99	76
	4	97	68
O. blandina×rubrinervis	1	96	75
	2	96	80
	3	96	.....

The *laeta* have hardly any empty grains, but the figures for *velutina* fall short of this, even as in other instances. In the last place, I counted the germs in the hybrids of the crosses with *Lamarckiana*, self-fertilizing their specimens of each of the types:

Cross	Parent number	Percentage of germs in seeds of		
		lucida	*Lamarckiana*	*rubrinervis*
O. rubrinervis×Lamarckiana	1	87	25	53
	2	91	34	59
	3	94	93	65
O. deserens×Lamarckiana	1	85	.....	.....
	2	86	.....	.....

The *lucida* have almost no empty grains; the figures for hybr. *rubrinervis* are the same as those for the mutant of that name, but those for the *Lamarckiana* type give an unexpected result. In two cases they are the same as for the species, but in the third the empty grains have almost wholly disappeared. This latter specimen has lost all the external marks of *O. deserens* and *O. rubrinervis*, but kept the absence of the lethal factors. Its progeny splits into *Lamarckiana*, *lucida*, and *rubrinervis*, and the first of these forms repeats the splitting in the following generation.

O. LAMARCKIANA NANELLA×RUBRINERVIS.—As in so many other cases, the crosses with dwarfs can give a verification of those with the species itself. In *Gruppenweise Artbildung* (p. 215) I have

described the pedigrees of two reciprocal crosses, both of which produced as a second hybrid the *subrobusta*. This was seen to split off, after self-fertilization, brittle plants and dwarfs. In 1915 I sowed some seeds of the *subrobusta* plants of 1907 mentioned in those tables, in order to compare their progeny with my newer cultures. I found for two specimens of *O.* (*nanella*×*rubrinervis*) *subrobusta* 38 and 45 per cent of dwarfs among 82 and 60 plants, and for two parents *O.* (*rubrinervis*×*nanella*) *subrobusta* 20 and 13 per cent of dwarfs among 60 and 46 individuals. The number of brittle plants, however, was very small, being two specimens for the first and one for the reciprocal group. It is possible that the germs of this type are weaker, and that some of them had died during the 7 years of their preservation. I self-fertilized one brittle specimen in each of the two main groups and had in 1916 two lots of 45 and 60 flowering plants, all of which were brittle and like their parents. They contained 9 and 8 per cent of dwarfs, the stems of which were likewise brittle at the time of flowering.[10]

Other races of *O. nanella* or other conditions may produce in the corresponding crosses brittle hybrids instead of *subrobusta*. I made the cross *O. rubrinervis*×*nanella* in 1905 with a dwarf mutant race of 1895 and the reciprocal one with the progeny of a dwarf which had arisen in 1911 from *Lamarckiana*, using in both cases the same family of *rubrinervis* as in all previous crosses. The first named cross gave 35 per cent *Lamarckiana*, 3 per cent *lucida*, and 62 per cent brittle *rubrinervis* among 68 specimens in 1913. The second cross yielded the same three types, but the percentage figures deviated widely. I had only 6 per cent *Lamarckiana* and 2 per cent *lucida*, but 92 per cent brittle *rubrinervis* among 140 plants, most of which flowered in August. The main result, however, is clear, namely, that the crosses between *O. rubrinervis* and *O. nanella* give three types of viable hybrids, one of which carries the visible marks of *O. rubrinervis*, but may be either brittle or tough.

I have made only one cross between *O. deserens* and a dwarf, taking this latter from the first of the two last mentioned families.

[10] By means of this the gap left in the second pedigree of p. 215 of my book is filled up, and both pedigrees are completed by the production of dwarfs from the *rubrinervis* specimens.

I crossed them in 1915 and had in 1916 a culture of 60 plants, among which 3 per cent were *lucida* and 97 per cent brittle *rubrinervis*. Other types failed, as was to be expected. The seeds of the two *lucida* plants contained 89 and 95 per cent of good germs.

Summing up the results of the crosses between *O. rubrinervis* and *O. nanella*, we see that they yield exactly the same hybrid types as those with *O. Lamarckiana* and in corresponding percentages.

CROSSES OF O. RUBRINERVIS WITH HETEROGAMIC MUTANTS.—Crosses with the pollen of these forms must simply confirm those with *O. Lamarckiana*, since their pollen carries mainly the same hereditary qualities as that of the parent species. I fertilized in 1913 two plants of my main race of *O. rubrinervis* with *O. cana*, two with the pollen of the *Lamarckiana*-like offspring of self-fertilized *scintillans*, and added the reciprocal cross of the latter combination. In the following table I shall call these offspring *scintillans-Lamarckiana*.

CROSSES OF *O. rubrinervis* WITH HETEROGAMIC MUTANTS

CROSS	NUMBER OF SPECIMENS	PERCENTAGE OF		
		Lamarckiana	*lucida*	*subrobusta*
O. rubrinervis×cana	60	32	38	30
O. rubrinervis×cana	57	53	32	15
O. rubrinervis×scintillans-Lamarckiana	60	13	3	84
O. rubrinervis×scintillans-Lamarckiana	60	7	10	83
O. scintillans-Lamarckiana×rubrinervis	84	7	4	89
O. scintillans-Lamarckiana×rubrinervis	34	15	9	76

About one-half of each group flowered in August. No brittle specimens occurred. The types were exactly the same as those derived from the cross between *O. rubrinervis* and *O. Lamarckiana*.

If the heterogamic types are used as female parents, the splitting of course will be more complicated. I fertilized a strong biennial specimen of *O. scintillans* with the pollen of a plant of *O. rubrinervis* and had in 1916 a culture of only 23 plants, all of which flowered in August. There were 5 types: 11 *Lamarckiana*, 2 *lucida*, 1 *sub-*

robusta, 9 *scintillans*, and 8 *oblonga*. The first three were the same as in previous crosses and confirm their result; the last two named types are the same as are always seen in the first generation of crosses of *O. scintillans* when this is used as the seed parent.

Moreover, in 1915 I fertilized 4 plants of my race of *O. lata* with *O. rubrinervis*, counted the *lata* and *albida* in their progeny in May 1916, and for want of space planted out only a part of the others, in order to distinguish the types, but without trying to determine percentage figures. Altogether I had 434 seedlings, among which 7 per cent were *lata* and 6 per cent *albida*. At the time of flowering I counted 23 *Lamarckiana*, 1 *lucida*, 20 brittle *rubrinervis*, besides 11 mutants (5 *oblonga*, 5 *obovata*, and 1 *scintillans*). No *subrobusta* occurred in these cultures. These results confirm those previously given.

SECOND AND LATER GENERATIONS.—Brittleness and dwarfish stature are recessive characters, and as such may be expected to be split off in the succeeding generations. For the crosses between *O. rubrinervis* and *O. nanella* this splitting has already been dealt with. For the other crosses our analytical formula for *O. Lamarckiana*×*rubrinervis* shows that the types *lucida* and *subrobusta* may be expected to produce a splitting, whereas the *Lamarckiana*-like hybrids cannot contain the necessary factors. The production of brittle plants from *subrobusta* had been observed in the case of the dwarfs, and so I studied in 1916 the progeny of three specimens of *lucida* from previous crosses.

SPLITTING PROGENY OF *O.* HYBR. *lucida;* CULTURES OF 1916

LUCIDA FROM	NUMBER OF SPECIMENS	PERCENTAGE OF	
		Tall plants	*deserens*
O. rubrinervis×scintillans	67	52	48
O. rubrinervis×scintillans	56	80	20
O. rubrinervis×Lamarckiana	106	53	47
Mean		62	38

Moreover, in 1916 I self-fertilized some specimens of *lucida* taken in the first generations of the crosses mentioned, sowed their seeds in 1917, cultivated all the seedlings until the time of ripening their first fruits, and counted them repeatedly during the summer. The

difference between the *deserens* and the *lucida* was very striking, the first reaching only half the height of the latter. I have broken the stems of all the plants in August, at the time of the last counting, and found all the *deserens* brittle and all the tall ones tough. The first were evidently *deserens* and not *rubrinervis*, as seen by the characters described for these two types. Among the tall ones, however, I have not succeeded in finding any difference, the type of *lucida* prevailing to the apparent exclusion of that of *O. Lamarckiana*. For each of the crosses mentioned in the following table I had 58–60 flowering specimens in August.

SPLITTING PROGENY OF HYBRID *lucida;* CULTURE OF 1917

LUCIDA FROM	PARENT NUMBER	PERCENTAGE OF	
		Tall plants	*deserens*
O. rubrinervis×O. Lamarckiana	1	50	50
	2	60	40
	3	48	52
O. deserens×O. Lamarckiana	1	55	45
	2	39	61
O. deserens×O. nanella	1	51	49
	2	41	59
Mean		49	51

Oenothera Lamarckiana mut. oblonga and mut. nanella

Our conception of *Oenothera rubrinervis* as a half mutant may be applied to *O. oblonga*, and explain its behavior in crosses in an analogous way. The main difference, as I have pointed out in *Gruppenweise Artbildung*, is that some types of hybrids, as we might expect, are constantly absent or suppressed, as I called it. If we assume this suppression to take place in the pollen before fecundation, the remaining phenomena are easily explained on this basis. It will be sufficient to review the facts given in my book, and to combine them with the results of some determinations of the amount of barren grains in the seeds of self-fertilized and crossed individuals.

The amount of empty seeds is about the same in *O. oblonga* as in *O. Lamarckiana*. For the cultures of 1911, mentioned in my book, I found among the seeds of two self-fertilized individuals 25 and 33 per cent of germs. Seeds of biennial plants collected in 1913 contained 30–18 and 17 per cent of germs; but seeds of annual

plants, saved in 1914 on two new mutants from *O. Lamarckiana* and on one from *O. cana*, gave only 6–5 and 6 per cent of germs. Annual specimens are always much weaker than biennial ones, and their fruits are often thin instead of club-shaped. These figures evidently point to a complete analogy with *O. Lamarckiana*.

The question whether the lethal factors are the same as in *O. Lamarckiana* may be answered by crosses with this species. I tried the seeds of a cross *O. oblonga*×*Lamarckiana*, of one of *O. oblonga*×*nanella*, both made in 1911, and of a cross of 1913 of *O. oblonga*×*O. cana*. I found 53–40 and 34 per cent of good germs. The figures do not essentially differ from those found for self-fertilized *Lamarckiana*, and thereby show that the lethal factors must be the same and simply inherited by *O. oblonga* from its parent species without change.

The ovules which produce empty grains after self-fertilization may develop into normal seeds after crosses with other species, even as in the case of *O. Lamarckiana* itself. *O. oblonga*×*biennis* gave 92 per cent of germs, *O. oblonga*×*atrovirens* (*cruciata*) 87 per cent, *O. oblonga*×*Hookeri* 90 per cent, and *O. syrticola* (*muricata*)× *oblonga* 90 per cent. Thus we see that in this respect also the lethal factors are the same as in *O. Lamarckiana*.

Our assumption is that *O. oblonga* arises by means of a mutation in the *Lamarckiana* gametes of our species, leaving the *velutina* gametes unchanged. The formula for self-fertilization, assuming the *oblonga* gametes to be suppressed in the pollen before fecundation, is as follows: (obl.+velu.)×velu.=obl.×velu.+velu.×velu. This explains the constancy of the mutant, since the *velutina*× *velutina* germs contain the same lethal factor on both sides and thus produce the empty grains. If we compare this formula with the results of the crosses described in my book (pp. 266–267), we find a complete harmony, as I shall now try to show.

Fertilized by *O. Lamarckiana* and analogous mutants, *O. oblonga* must give (obl.+velu.)×(Lam.+velu.)=obl.×Lam.+obl.×velu. +velu.×Lam.+velu.×velu.=25 per cent empty grains+25 per cent *oblonga*+25 per cent *Lamarckiana*+25 per cent empty grains. The expectation is therefore for two types and these in equal proportions. The two types always appeared, and no others besides

them, but the percentage figures are very variable. I found them as follows:

Cross	Parent number	Percentage of	
		oblonga	*Lamarckiana*
O. oblonga×Lamarckiana	1	4	93
O. oblonga×Lamarckiana	2	4	96
O. oblonga×Lamarckiana	3	14	85
O. oblonga×nanella	1	15	80
O. oblonga×nanella	2	46	14
O. oblonga×scintillans	1	81	17

The reciprocal crosses cannot produce any *oblonga*, since this is assumed to be suppressed in the pollen. The only exception is *O. scintillans*, which gives rise to a high amount of *oblonga* after self-fertilization, and therefore may produce the same mutant after a cross. I found as follows:

Cross	Percentage of	
	oblonga	*Lamarckiana*
O. Lamarckiana×oblonga	0	100
O. nanella×oblonga	0	100
O. lata×oblonga	0	100
O. scintillans×oblonga	18	82

The pollen of *O. oblonga* must produce, after crosses with different species, only *velutina*, as is easily seen from our formula. No *oblonga* and no *laeta* are to be expected. *O. biennis*, *O. syrticola*, *O. Cockerelli*, and *O. Hookeri* fecundated with *O. oblonga* uniformly gave this result. The reciprocal crosses, however, must give a splitting, the *laeta* hybrids assuming the characters of *O. oblonga*. The percentages should be about 50, but in my experiments there was much fluctuation in this respect. I found as follows:

Cross	Parent number	Percentage of	
		oblonga	*velutina*
O. oblonga×biennis Chicago	1	8	92
O. oblonga×biennis Chicago	2	16	84
O. oblonga×biennis Chicago	3	38	62
O. oblonga×Cockerelli	1	41	59
O. oblonga×Hookeri	1	11	89
O. oblonga×Hookeri	2	24	75

Crosses with *O. rubrinervis* also yield the expected result. This would be in one direction (obl.+velu.)×(deserens+velu.)=obl.×des.+obl.×velu.+velu.×deserens+velu.×velu.=25 per cent (*obl.×des.*)+25 per cent *oblonga*+25 per cent *rubrinervis*+25 per cent empty grains. I have not as yet tried the cross between *O. oblonga* and *O. deserens*, however, and thus must leave undecided the question as to which characters will dominate in this hybrid. As a matter of fact, I found 20 per cent *oblonga* and 80 per cent *rubrinervis* and no other types. The reciprocal cross must give (des.+velu.)×velutina=des.×velu.+velu.×velu.=50 per cent *rubrinervis*+50 per cent empty grains. Only *rubrinervis* have been observed in this culture.

Crosses with the pollen of *O. biennis* must give *oblonga*×*biennis* +*velutina*×*biennis*. The former is intermediate between the parents, whereas the second is the same as the hybrid type *Lamarckiana* ×*biennis*. I found in one cross 65 per cent *oblonga* (partly dwarfish) and 35 per cent hybrids of the second type. In another instance, however, the *oblonga* failed from some unknown reason.

With those species which ordinarily produce the twins *densa* and *laxa* the pollen of *O. oblonga* must evidently give only the latter type. This has been the case in three trials with *O. biennis Chicago* and in one with *O. atrovirens* (*cruciata*).

For further details and for the constancy or splitting in the second generation I must refer the reader to the pages of my book already quoted. These results, however, show clearly that all the facts hitherto ascertained confirm the formula assumed for the self-fertilization, and thereby the analogy with the phenomena observed in *O. rubrinervis*.

Summing up this discussion we may say, therefore, that *O. oblonga* arises through a mutation of the typical sexual cells of *O. Lamarckiana*, leaving the *velutina* gametes and also the lethal factors unchanged, but producing, besides the externally visible marks of the mutant, a suppression of the mutated pollen grains.

On the other hand, *O.* mut. *nanella* seems to arise through mutations in the *velutina* gametes of *O. Lamarckiana*, as is shown by the fact that the *laeta* do not split off dwarfs, whereas the *velutina* regularly do so. The figures given in my book for the crosses with *O. nanella* may be calculated in the same way, and

will be found to comply with the views proposed in this article. It would lead us too far, however, to reproduce these calculations here.

In all these cases the conception that mass mutation is the chief cause of the production of twin hybrids evidently makes the supposition of a labile condition of the factor for *laeta* superfluous. It seems desirable, therefore, to lay stress on the fact that this supposition does not rest on the phenomena observed in the production of these twins. It is mainly derived from other observations, and some of them may be briefly repeated here in order to make this point clear. They refer to the brittleness of *O. rubrinervis* and *O. deserens* and to the dwarfish stature of *O. nanella*.

In crosses brittleness behaves in three different ways. With *O. biennis Chicago* and *O. Cockerelli* it is recessive to the tough structure of the fibers, since it fails in the first generation and reappears in the second in ratios corresponding to Mendel's law. In crosses with *O. Lamarckiana* it is sometimes dominant and sometimes recessive, as has been shown. In *O. rubrinervis* and *O. deserens* the toughness is wholly absent. From these and other facts it is clear that at least three conditions of this factor are possible. I call them active, labile, and inactive. Whether the labile condition is due to linkage or to some other cause is as yet an open question, which, however, has no influence upon the main contention. The combination "active×inactive" is assumed to be responsible for Mendelian crosses, but the combination "labile×inactive" may cause a splitting in the first generation and produces, as a rule, constant hybrids. The two types of first generation hybrids appear in variable numerical proportions according to different circumstances. If one of the groups is so small as not to be represented in every 100 specimens, the splitting may seem to fail, and such extremes are of common occurrence. This would explain the dominance of an evidently recessive character.

The case is exactly the same for the dwarfish stature. The factor for tallness must be in the inactive condition in the dwarfs, but in the active condition in *O. rubrinervis*, since the crosses between these two types follow Mendel's law. In *O. Lamarckiana*,

however, it is labile, since tall and low specimens appear in the first generation of its cross with *O. nanella*. In many ternary crosses of hybrids of this mutant the dwarfish stature dominates over the tall condition, but the dominance is not always absolute and sometimes 3–5 per cent of tall specimens appear among the dwarfs, as I have shown in *Gruppenweise Artbildung*. This fact evidently supports our conception.

The conclusion from this discussion is that since brittleness and dwarfish stature are in some cases recessive to and in other cases dominant over their antagonists, these latter must be sometimes in the active and in other instances in the labile condition.

Summary

1. *Oenothera rubrinervis* is a half mutant, produced by the copulation of a mutated gamete with a normal *velutina* gamete of *O. Lamarckiana*.

2. In consequence, it produces about one-fourth empty grains, a mass mutation of about one-fourth pure or double mutants, and one-half specimens of *O. rubrinervis*, which will repeat the splitting.

3. The pure or double mutant is called *O.* mut. *deserens*. It is very similar to *O. rubrinervis*, but the leaves of its young rosettes and the bracts of its flower spike are broader and more even.

4. *O.* mut. *deserens* is constant from seed. It has no hereditary empty grains.

5. The formula for the self-fertilization of *O. rubrinervis* is therefore *O.* (*deserens*+*velutina*) = *des.*×*des.*+*velu.*×*velu.*+*des.*×*velu*. The first combination gives the mass mutation, the second the empty grains, the third the normal plants of *O. rubrinervis*.

6. In crossing with other species the two kinds of gametes will produce twin hybrids, as, for example, *laeta* and *velutina*. This assertion has been controlled by making the corresponding crosses of *O.* mut. *deserens* and *O.* mut. *velutina*. The first produce the *laeta* and the second the hybrid *velutina*. The result of a cross of *O. rubrinervis* is equal to the sum of these two crosses.

7. Outside of the mass mutability into *O. deserens*, *O. rubrinervis* is not known to mutate to any noticeable degree. This shows that

the internal constitution, which causes the mass mutation, is not in itself a cause for further mutability.

8. The constitution of the gametes of *O. rubrinervis* can directly be proven by a cross with *O. deserens*, since *O. rubrinervis* = (*deserens* + *velutina*) × *O. deserens* produces *O. deserens* and (*O. deserens* × *velutina*) or *rubrinervis*.

9. Crosses of *O. rubrinervis* with *O. Lamarckiana* give three types of hybrids, besides about one-fourth empty seeds. One type exactly resembles *O. Lamarckiana* and is constant in its progeny. A second type called *lucida* has broader and more shiny leaves, and after self-fertilization splits off brittle specimens. The third type is either *subrobusta* or *rubrinervis*, and in the first case may produce the brittle form in the second generation. All these phenomena are easily explained by the proposed formula for the constitution of *O. rubrinervis* as a half mutant. They were confirmed by means of crosses with *O. nanella* and some other mutants.

10. *O. oblonga* is quite analogous to *O. rubrinervis*, since it must arise through a mutation of the typical sexual cells of *O. Lamarckiana*, leaving the *velutina* gametes unchanged. Contrary to *O. rubrinervis*, however, the two lethal factors remain in their condition, and moreover the mutated gametes must be assumed to become suppressed in the pollen of the mutant.

11. *O. nanella* seems to arise through mutations in the *velutina* gametes of *O. Lamarckiana*, since after crosses with other species or mutants it is not split off by the *laeta* hybrids, but only by those of the type *velutina*.

LUNTEREN, HOLLAND

NOTES ON AMERICAN WILLOWS. III

A CONSPECTUS OF AMERICAN SPECIES AND VARIETIES OF SECTIONS RETICULATAE, HERBACEAE, OVALIFOLIAE, AND GLAUCAE

CAMILLO SCHNEIDER

In this third article, as I said in my first paper,[1] a key will be given containing the species treated in the first two papers, and also those of the sections RETICULATAE and HERBACEAE (RETUSAE), together with a few other species the systematic position of which is not yet fully understood, but which are best placed near one of these groups. I have tried to prepare two separate keys for the determination of the male and female plants as I did in "Conspectus analyticus Salicum Asiae orientalis Himalayaeque" in SARGENT, Pl. Wils. 3:73. 1916. Typical complete specimens are not always at hand, and without them even such a good key as that given by COVILLE (in Proc. Wash. Acad. Sci. 3:300. 1901) to the Alaskan willows is insufficient to determine species. To make a key to the sections only proves likewise of little value owing to the great difficulty of exact limitation of the groups, as I shall explain later.

Clavis specierum

1. SECUNDUM SPECIMINA FEMINEA

A. Ovaria (pedicellis inclusis) etiam juvenilia glaberrima.

I. Folia utrinque concoloria, viridia et stomatifera, minima vel parva; amenta serotina, vulgo pauciflora; bracteae pl.m. concolores, flavescentes vel violascentes, vix vel sparse brevi-pilosae; fruticuli minimi prostrati (sed vide 7. *S. Peasei*).

Folia semper crenato-dentata, utrinque tenuiter reticulata, anni praeteriti nunquam persistentia.

Ramuli floriferi tenuissimi, breves, fere semper bifoliati; bracteae flavescentes, sparse pilosae.....8. *S. herbacea*

Ramuli floriferi crassiores, longiores, 2–4-foliati; bractae fuscescentes, albido-pilosae.....7. *S. Peasei*

[1] BOT. GAZ. 66:118. 1918.

Folia integerrima, adulta sicca per secundum annum vel diutius persistentia.

Nervi laterales foliorum utrinque pl.m. elevati, venulae etiam prominulae (confer etiam 10. *S. phlebophyllam*, cujus fructus interdum glaberrimi sunt) . . 9. *S. rotundifolia*

Nervi laterales foliorum superne tenuissime incisi, subtus prominentes, venulae haud visibiles . . 11. *S. Dodgeana*

II. Folia discoloria, subtus distincte pallidiora, pl.m. glaucescentia (saepissime pruinosa); fruticuli repentes vel parvi, erecti.

Bracteae concolores, flavescentes, glabrae vel sparse tantum ciliatae.

Fruticuli parvi, erecti, ramis non prostratis et radicantibus; styli distincti, quam stigmata brevia bifida longiores, haud vel tantum apice fissi; folia circiter 3–5plo longiora quam lata.

Folia superne cito margine excepto glabra, stomatifera 21. *S. chlorolepis*

Folia superne infimis exceptis pl.m. villosula, estomatifera . . . . . 22b. *S. brachycarpa* var. *glabellicarpa*

Fruticulus depressus, ramis prostratis radicantibus; stylus brevissimus, vulgo bifidus stigmatibus bifidis haud longior; folia satis crassa, vix $1\frac{1}{2}$plo longiora quam lata 3. *S. leiolepis*

Bracteae pl.m. bicolores, ad apicem vel fere totae fuscae, pl.m. longe sericeo-pilosae; fruticuli parvi, prostrati, ramis radicantibus.

Ovaria etiam juvenilia distincte pedicellata; pedicellus fructuum glandulam late ellipsoideo-rectangularem vel subquadratam circ. 2plo superans; stylus distinctus, apice bifidus stigmatibus brevibus oblongis bifidis subduplo longior; folia superne haud stomatifera, margine vulgo sparse et saepe indistincte denticulata 18. *S. arctophila* f. *lejocarpa*

Ovaria subsessilia vel breviter pedicellata, pedicello etiam fructuum quam glandula pl.m. breviore vel vix sublongiore.

Folia pl.m. glanduloso-crenato-denticulata (saltem ad medium et apicem), rarius subintegerrima, superne sto-

matifera, adulta marcescentia partim diu persistentia; stipulae saepe distinctae; stylus apice bifidus stigmatibus brevissimis bifidis 2–2½plo longior....6. *S. Uva-ursi*
Folia integerrima, rarissime basim versus paucidentata; stipulae nunquam distinctae.

Amenta cylindrica, 3–4plo longiora quam lata, 3–5 cm. longa (saltem basi) sublaxiflora; folia majora ultra 3 cm. longa, superne non stomatifera
15. *S. arctica* f. *glabrata*

Amenta etiam fructifera vix ad ½plo longiora quam lata, densiflora; folia etiam maxima vix ultra 2.5 cm. longa vel superne stomatifera.

Stylus satis brevis, stigmatibus mediocribus vix longior; fructus maturi vulgo pl.m. glaucescentes; folia superne (in var. *camdensi* excepta) haud stomatifera, matura subcrassa, subtus conspicue elevato-reticulata.....16. *S. ovalifolia*
Stylus elongatus tenuis, stigmatibus angustis longis saepe pl.m. longior; fructus maturi vix glaucescentes; folia superne stomatifera, matura tenuiora, subtus vix conspicue reticulata....17. *S. stolonifera*

B. Ovaria (interdum tantum partim vel nonnisi pedicelli) pl.m. dense pilosa; fructus saepe glabriores vel partim glabri.

I. Folia (sub anthesi perfecte evoluta) utrinque concoloria, viridia, aequaliter stomatifera, integerrima; fruticuli minimi repentes.

Ramuli floriferi breves, tenuissimi, vulgo 2-foliati; folia utrinque tenuiter reticulata, adulta sicca non persistentia; amenta pauciflora, vel multiflora; ovaria interdum tantum ad apicem pilosa, pl.m. sessilia; stylus distinctus, stigmatibus vulgo longior; glandula 1.....5. *S. polaris*
Ramuli floriferi 2–4-foliati; folia adulta marcescentia parenchymate evanescente plures annos persistentia; amenta pluriflora, cylindrica; ovaria saepius distinctius pedicellata; glandula etiam dorsalis interdum adest (confer etiam 9. *S. rotundifoliam* f. *pilosiusculam*).....10. *S. phlebophylla*

II. Folia subtus discoloria, pallidiora vel pl.m. glaucescentia, vulgo pruinosa, vel plantae aliis signis diversae.

a. Folia circumcirca satis dense minute glanduloso-serrata, obovata, fere glabra; stipulae distinctae, lanceolatae, serratae; amenta pedunculo excluso 5–6 cm. longa, 10–15 mm. crassa; stylus distinctus, stigmatibus circ. 2plo longior; planta prostrata.....29. *S. Chamissonis*

b. Folia integerrima vel pl.m. crenato-denticulata, vel plantae aliis signis diversae.

1. Amenta serotina, pseudoterminalia, anguste cylindrica vel minima pauciflora, pedunculis nudis iis saepe aequilongis suffulta; bracteae breviter (rarius longius) pilosae, pl.m. concolores, flavescentes vel violascentes; ovaria sessilia vel subsessilia; styli (*S. venusta* excepta) brevissimi vel nulli, stigmata brevia vel brevissima; glandulae 2 vel interdum plures pseudodiscum lobulatum formantes; folia satis crassa, superne pl.m. inciso-reticulata, rugosa, haud stomatifera (*S. venustae?*), subtus distincte elevato-reticulata, vulgo pl.m. longe petiolata.

Folia coriacea, pleraque vix longiora quam lata vel ultra 4 cm. longa, superne conspicue inciso-reticulata, rugulosa; bracteae intus pl.m. brevipilosae vel utrinque sericeae.

Frutex prostratus; folia cito glaberrima vel rarius pilis paucis sericeis obsita, vix ad 5.5:5 cm. magna; petioli elongati, ad 3 cm. longi; bracteae intus tantum brevipilosae; fructus vix ultra 4.5 mm. longi

1. *S. reticulata*

Frutex prostratus vel erectus; folia etiam adulta subtus dense sericea vel majora, oblongiora et margine pl.m. distincte crenulata, vel petioli breves gemmis vix longiores: bracteae utrinque pl.m. sericeo-pilosae; fructus 5–7 mm. longi.....2. *S. vestita*

Folia tenuiora (chartacea), minima vel distincte longiora quam lata, vix ultra 3.5:2 cm. magna, superne vix vel indistincte inciso-reticulata; bracteae glabrae vel tantum margine basique pilosae, rarius etiam extus pl.m.

pilosulae; frutices prostrati, interdum minimi suffruticulosi (confer etiam 31. *S. venustam* cujus specimina nondum vidi et quae stylo elongato filiformi fusco distincta dicitur; tantum a Sitka reportata)

4. *S. nivalis* et var. *saximontana*

2. Amenta coetanea, rarius pl.m. serotina, lateralia, ovata vel cylindrica, multiflora, rarius parva et pauciflora, sed pedunculi semper foliati; folia pl.m. tenuiter papyracea, superne nunquam inciso-reticulata.

a) Bracteae bicolores, apice vel pro parte maxima fuscae, versus apicem longe sericeae (id est pilis longis sericeis quam bractea vix vel paullo brevioribus instructae), interdum apice tantum ciliatae; fruticuli fruticesque parvi ramis ut videtur semper prostratis (confer etiam 28. *S. lingulatam* speciem valde incertam).

Stylus sub nullus, quam stigmata divaricata bifida duplo brevior; amenta parva circ. 10 mm. longa, ovoidea vel ovato-globosa; bracteae atrae, extus sparse sericeae vel partim glabrae; ovaria breviter pedicellata, albo-sericeo-villoscula; folia ovata vel late lanceolata, obtusa, rigida vix ad 12 mm. longa....30. *S. glacialis*

Stylus semper distinctus, stigmatibus aequilongus vel vulgo longior.

Folia sicca anni praeteriti pl.m. persistentia, lingulata, lineari- vel anguste oblanceolata (vel lanceolata apice subplicato-acuminata), vix ultra 18:5 mm. magna, superne stomatifera, subtus paullo pallidiora; amenta parva, etiam fructifera vix ad 2.5:0.9 cm. magna pedunculis 0.5–3 cm. longis exclusis; bracteae laxe sericeae, extus saepe glabrescentes; (ovaria et) fructus subsessiles, circ. 4–5.5 mm. longi, pl.m. villoso-tomentosi.....12. *S. cascadensis*

Folia adulta haud persistentia et plantae aliis signis diversae.

Stigmata linearia, elongata, stylo tenui satis longo pl.m. 2–3plo breviora; ovaria fructusque saepe

tantum ad apicem sparse pilosi, ceterum ut supra sub *S. stolonifera* indicata

17. *S. stolonifera* f. *subpilosa*

Stigmata brevia vel oblonga sed vix linearia vel plantae aliis signis diversae.

Folia subtus (in sicco) paullo pallidiora (haud distincte glaucescentia vel albescentia), leviter elevato-nervata sed vix reticulata, laevia, petiolis vix 5–6 mm. longis instructa, vulgo lanceolata vel elliptico-lanceolata, utrinque acuta vel apice obtusa, superne stomatifera et interdum fere inciso-nervata, etiam maxima vix ad 4:1.8 cm. magna, integerrima (rarissime versus basim parce denticulata); stipulae nullae vel minimae, caducae; amenta (pedunculo excluso) 2–4.5 (in var. *caespitosa* interdum ad 6) cm. longa et fructifera ad 1.3 cm. crassa; ovaria subsessilia, dense sericeo-villosa; stylus distinctus, saepe apice breviter bifidus, stigmatibus oblongis bifidis vulgo duplo rarius 3plo longior; glandula ventralis oblonga, ovoideo-conica; fructus pedicello brevi glandulam siccam subaequante excluso 4–5 mm. longi; fruticulus ramulis hornotinis flavescentibus tenuibus satis brevibus . . . 13. *S. petrophila*

Folia subtus distincte discoloria, glaucescentia, pruinosa, superne haud stomatifera vel majora, diversiformia vel plantae aliis signis diversae.[2]

Glandula ventralis satis brevis et lata, vix duplo altior quam lata, apice late truncata, pedicello fructuum duplo brevior; amenta submatura vel fructifera (3–)5–10:1.2–1.6 cm. magna; ovaria tenuiter villoso-tomentella; styli distincti, apice bifidi, stig-

[2] It is difficult to indicate in such a key the differences between *S. petrophila* and *S. anglorum* and its different forms with sufficient clearness. See my remarks under those species in my first paper (*l.c.*).

matibus oblongis bifidis paullo vel duplo (rarius fere triplo) longiores; fructus pedicello excluso 6.5–8 mm. longi; folia superne estomatifera, margine vulgo partim sparse et saepe obsolete denticulata, forma variabilia, majora latiora ad 3–4(–5):2.5(–3) cm. magna; frutex procumbens ramulis saepe satis elongatis, 2–3 mm. crassis (si glandula est brevis et lata sed pedicello brevior, confer 18a. *S. hudsonensem*) . . . . . 18. *S. arctophila*

Glandula oblonga, vulgo 2½–4plo longior quam lata et pedicelli etiam fructuum quam glandula pl.m. breviores vel rarius sublongiores vel plantae aliis signis diversae.

Amenta fructifera ellipsoideo-globosa, circ. 1–1.5:1.5 cm. magna; folia subcoriacea, late ovalia vel obovato-rotunda, vix ultra 1.8:1.5 cm. magna, superne estomatifera, in sicco tenuiter reticulata, subtus valde elevato-reticulata, utrinque (saltem initio) ut ramuli novelli villosula

16b. *S. ovalifolia* var. *pubescens*

Amenta fructifera cylindrica, vulgo longiora, tenuiora; folia tenuiora vel majora, subtus nunquam conspicue elevato-reticulata.

Folia superne haud stomatifera,[3] vulgo obovata vel obovato-oblonga, apice rotundata ad subacuta vel plicato-acuta, basi sensim vel subito attenuata, obtusa vel interdum rotundata, majora satis evoluta 3–6:2–4 cm. magna; petioli 9–20 mm. longi; stipulae in ramulis vegetis ovato-lanceolatae vel lanceolatae,

[3] With the exception of *S. arctica* var. *subcordata*, which, however, is easily distinguished from any of the forms of *S. anglorum* by its much larger leaves and longer stouter catkins.

integrae vel subdenticulatae, 2–12 mm. longae; amenta sub anthesi 2.5–4 cm. longa, bracteis atris dense longe sericeis conspicua, fructifera 6:1.3 ad 9:1.8 cm. magna; ovaria sessilia vel subsessilia, sericeo-villosa; styli distincti, vulgo integri, quam stigmata oblonga bifida 2–2½plo longiores; fructus pedicello brevi glandula ⅔ ad vix breviore (rarissimo sublongiore) excepto (6–)8–10 mm. longi (confer etiam 16c. *S. ovalifoliam* var. *subarcticam* et 18a. *S. hudsonensem*)

15. *S. arctica* et varietates

Folia superne stomatifera, vulgo minora, valde variabilia (vide formas sub *S. anglorum* enumeratas); petioli vix ultra 10 mm. longi; stipulae nullae vel minores; amenta etiam fructifera vix ad 5.5:1.5–1.8 cm. magna, saepe distincte minorà, tenuiora; fructus ad 7–8 mm. longi pedicello subnullo vel glandula 2 ad ⅓plo breviore excluso (si folia sunt estomatifera sed plantae aliis signis haud diversae, confer etiam 18a. *S. hudsonensem*)

14. *S. anglorum* et varietates

β) Bracteae concolores, flavescentes, stramineae vel brunnescentes (rarius subbicolores, apice violaceae vel leviter fuscae), semper breviter sericeo-villosulae (id est pilis quam bractea brevioribus instructae), intus interdum glabratae.

(1) Petioli brevissimi, 1–2 vel vix ultra 2.5 mm. longi, gemmas bene evolutas non superantes et stipulae petiolis aequilongae vel duplo longiores; amenta florifera minima vel parva, etiam fructifera vix ad 2.5:1–1.2 (vel in *fullertonensi* ad 4:1.3) cm. magna.

Frutex prostratus ramis repentibus; folia breviter

lanceolata, elliptico-oblonga vel oblonga, utrinque pleraque acuta, 1:0.5 ad 3:0.9–1.2 cm. magna, superne vulgo sparse stomatifera; stipulae distinctae; ovaria sessilia vel subsessilia, villosulo-tomentosa; stylus satis brevis, integer vel apice bifidus stigmatibus oblongis bifidis subaequilongus; bracteae oblongae; glandula dorsalis anguste conica, interdum pl.m. bifida, iis duplo brevior; fructus subsessiles, 4.5–6 mm. longi

19. *S. fullertonensis*

Frutices parvi erecti, ramis saepe satis brevibus subtortuosis divaricatis vel subelongatis strictioribus et plantae aliis signis diversae.

Folia superne stomatifera, oblonga, ad 3:1 cm. magna adulta etiam subtus satis glabrata; bracteae intus glabrae, late ovales vel obovales; stylus distinctus quam stigmata vulgo ultra duplo longior; ovaria sessilia, saepe infra medium glabra; ramuli hornotini satis glabrescentes.....21b. *S. chlorolepis* var. *antimima*

Folia superne haud stomatifera, magis (saltem subtus) villosa vel sericeo-villosa; ramuli hornotini semper pl.m. dense villoso-tomentosi; bracteae vulgo utrinque pilosae vel interdum extus glabriores.

Ramuli hornotini densissime albo-sericeo-villosi; styli ovariorum sessilium, brevissimi, vix ad 0.5 mm. longi, stigmatibus brevibus; folia oblongo-lanceolata vel anguste ovato-lanceolata, apice (infimis exceptis) pl.m. acuta, basi rotundata vel obtusa, 1.5:0.5 ad 3.5:0.9–1 cm. magna, novella utrinque sericeo-villosa; species satis imperfecte cognita.....20. *S. niphoclada*

Ramuli hornotini vel vulgo tantum novelli minus dense griseo-vel subflavescenti-sericeo-villosi; styli distinctiores, stigmatibus aequi-

longi vel saepe distincte longiores; folia elliptico-oblonga, oblanceolata, rarius ovato- vel elliptico-lanceolata, interdum obovato-oblonga, apice obtusiuscula vel subito breviter acuta, basi late cuneata vel obtusa, rarius rotundata ad subcordata, sub anthesi saepe minima vel parva, subspathulata vel lineari-lanceolata, ad 2.5–3:(0.6–)1 vel 3.4:0.8 vel ad 3:1.1 (maxima ad 4.5:1.2) cm. magna; amenta sub anthesi vix ultra 10:4 mm., fructifera 1.5:0.8 ad 2.5:1(1.2) cm. magna; fructus subsessiles vel pedicello glandula vulgo duplo breviore suffulti, 5–7 mm. longi
22. *S. brachycarpa*

(2) Petioli gemmis vel stipulis longiores, amenta etiam florifera longiora vel plantae alio modo diversae. Folia parva vel mediocra, majora apice ramulorum vulgo haud ultra 4:1.8 cm. magna, lanceolata, oblanceolata, elliptico-lanceolata, anguste elliptica ad obovato-lanceolata, rarius elliptico-vel obovato-oblonga, apice acuta vel subacuta, basi cuneata ad rotundata, integerrima (infima minima tantum brevissime glanduloso-denticulata), superne stomatifera, novella pl.m. tenuiter griseo-villosula, demum glabrescentia vel subglabrata, subtus discoloria, glaucescentia, ut superne vel densius villosula (sed pubescentia satis variabili); stipulae nullae vel valde reductae; amenta sub anthesi 8–15:5 ad 25:6 mm., fructifera ad 2–3:1–1.5 cm. magna; fructus 6.5–8 mm. longi, pedicello brevi quam glandula duplo breviore (rarius ea subaequilongo) excluso; ramuli novelli griseo-villosuli vel subtomentosi, annotini saepe subglabri, purpurasentes vel fere nigro-castanei vel ut vetustiores epidermide griseo-flavescente pl.m. secedente obtecti (conf. etiam 23. *S. desertorum*, speciem tantum incomplete cognitam).....24. *S. pseudolapponum*

Folia majora vel latiora vel superne haud stoma-

tifera vel amenta fructifera majora et fructus 8–10 mm. longi pedicellis glandulam ad duplo superantibus.

Folia superne haud stomatifera.[4]

Fructus pedicello subnullo vel brevi glandulam haud superante suffulti, 6–8(–10) mm. longi; amenta sub anthesi 1–2.5:0.7 cm., fructifera ad 3–5:1.2–1.5 cm. magna pl.m. densa; folia (var. *atra* excepta) tantum ½ ad 2½plo longiora quam lata, elliptica, ovalia, obovato-elliptica, obovato-oblonga, vel ovato-elliptica, apice pl.m. obtusa vel breviter acuta, basi obtusa vel late cuneata ad subcordata, 3:2 vel 3.5:2.5 vel 4.5:2–2.3 ad 6:2.8 cm. magna, novella pubescentia (minimis infimis exceptis) pl.m. villosa induta, superne glabrescentia, rarius adulta utrinque glaberrima.....26. *S. cordifolia*

Fructus pedicello glandulam vulgo ¼ ad 2plo superante instructi, 7–8(–9) mm. longi; amenta sub anthesi 2–4:0.8–1 cm., fructifera 3.5–7:1.5 cm. magna, basi saepe satis laxiflora; folia vulgo 2½ ad ultra 4plo longiora quam lata, lanceolata, oblanceolata, elliptico-oblonga, obovato-oblonga vel obovato-elliptica, apice obtusa vel vulgo acuta vel fere breviter acuminata, basi obtusa vel subito sensimve cuneata, mediocra 4.5:2 ad 5:1.5 vel 7:2.3 cm. magna, novella pubescentia satis sericea induta, superne paullo vel omnino glabrescentia, subtus saepe glabriora 25. *S. glaucae* varietates

Folia superne stomatifera, ceterum ut in vol. 66, p. 349 descripta.....27. *S. anamesa*

[4] Owing to the variability of the nos. 24–26 and our insufficient knowledge of the Greenland forms I cannot avoid using this anatomical character in distinguishing *S. anamesa* from the other two species. But *S. anamesa* is apparently a species met with only in Greenland, and therefore the arrangement of the key will not be inconvenient to most of the students of American willows.

2. SECUNDUM SPECIMINA MASCULA[5]

A. Filamenta omnino glabra

I. Stamen unicum (rarissime stamina 2 adsunt); bracteae pl.m. purpurascentes et apice atrae, pilis longis argenteis sericeae; folia adulta glabra, discoloria, superne pl.m. nitida et stomatifera, pl.m. crenato-denticulata, rariter ad 2.5 cm. longa; frutex depressus vel prostratus .....6. *S. Uva-ursi*

II. Stamina semper 2.

a. Fruticuli minimi, suffruticosi, ramulis tenuissimis, fere semper radicantibus; folia utrinque concoloria v. subconcoloria, etiam superne stomatifera, minima vel parva, rarius ultra 25 mm. longa latave; amenta serotina, tenuia, pauci- (rarius multi-) flora.

Folia utrinque obtusa vel acutiuscula (cuneata), integra, nervis primariis superne tenuissime incisis subtus prominentibus, ceterum enervia, 5–8:3–4 mm. magna; amenta 3–5-flora, rhachi bracteisque concoloribus glabris vel parcissime pilosis; glandulae 2.....11. *S. Dodgeana*

Folia utrinque rotundata vel basi cordata vel utraque facie distincte (sed saepe tenuiter) reticulata.

Ramuli breves floriferi fere semper bifoliati; folia adulta sicca haud per secundum annum persistentia; ramuli vetustiores 1–2 mm. crassi.

Bracteae glabrae subglabraeve, concolores, flavescentes vel violascentes; glandulae 2; folia semper crenato-serrata.....8. *S. herbacea*

Bracteae sericeo-villosulae, fuscae, pl.m. bicolores; glandula 1, ventralis; folia saepissime integerrima 5. *S. polaris*

Ramuli floriferi 2–5-foliati; folia adulta sicca pl.m. marcescentia, fuscescentia et per secundum annum persistentia, integerrima; glandulae fere semper 2 (in *S. cascadensi* ut videtur tantum 1).

[5] Of the following species the male plant is still unknown: *fullertonensis*, *hudsoniensis*, *leiolepis*, *lingulata*, *Peasei*, and *venusta*.

Amenta minima, 3–8-flora; folia vulgo orbicularia vel late ovalia, utrinque rotundata, vix ad 11:10 mm. magna, adulta sicca anno secundo decidua
9. *S. rotundifolia*

Amenta multiflora, ad 23 mm. longa; folia adulta plures annos persistentia vel pl.m. lineari-lanceolata.
Folia elliptica, obovato-oblonga vel late spathulata, apice rotundata vel breviter acuta, basi cuneata, subtus vix pallidiora, ad 15:9 mm. magna.....19. *S. phlebophylla*
Folia lingulata, lineari vel anguste lanceolata (vel oblanceolata), apice vulgo subplicato-acuminata, ad 18:5 mm. magna, subtus subpallidiora
12. *S. cascadensis*

b. Fruticuli vel frutices vel folia discoloria vel plantae alio modo diversae.

1. Bracteae pl.m. discolores, apice vel pro parte maxima fuscae, versus apicem longe sericeae (pilis longis sericeis quam bractea vix vel paullo brevioribus instructae), interdum apice tantum longe ciliatae; fruticuli vel frutices parvi, ramis prostratis, pl.m. radicantibus vel subterraneis, ramulis tantum floriferis pl.m. adscendentibus, vix ad 15–20 cm. altis (vel in *S. arcticae* formis interdum altioribus); si folia sunt tenuiter sed dense et acute glanduloso-serrulata, vide
29. *S. Chamissonis*

α) Folia subtus (in sicco) paullo pallidiora, leviter elevato-nervata, sed vix reticulata ceterum ut in p. 56 descripta; amenta 1–2.5 cm. longa, vix ad 1 cm. crassa, pluri- vel multiflora; glandula ventralis pl.m. elongato-conica, dorsalis saepe nulla
13. *S. petrophila*

β) Folia subtus distincte discoloria, glaucescentia vel albescentia, adulta pl.m. reticulata vel longius petiolata vel majora et forma diversa (specimina mascula specierum sequentium sine speciminibus

femineis accurate discernere saepe impossibile est).[6]

(1) Glandula ventralis satis brevis lataque, vix 2plo longior quam lata, apice late truncata, quam bractea obovata vulgo $2\frac{1}{2}$–3plo brevior;[7] amenta 2–2.5:0.8–1 cm. magna; folia tantum novella subtus sparse sericea, cito glabra, superne estomatifera, ceterum ut in p. 57 descripta; petioli vix ultra 8 mm. longi

18. *S. arctophila*

(2) Glandula ventralis pl.m. anguste ovato-rectangularis vel anguste conica, apice saepe leviter incrassato truncata, quam bractea vix duplo brevior vel folia superne stomatifera, semper integerrima vel plantae aliis signis diversae.

Amenta perfecte evoluta vix ultra 1.5:0.8 cm. magna; folia matura satis crasse papyracea, subtus pl.m. perspicue et anguste reticulata, vulgo elliptica, late elliptica, obovalia vel rotundata, vix ultra 2.5:1.2–2 cm. magna; stipulae nullae (vel minimae punctiformes) (si folia superne stomatifera confer. etiam 14. *S. anglorum* formas et 30. *S. glacialem* speciem valde incomplete cognitam).

Folia superne pl.m. stomatifera; ramuli annotini hornotinique vulgo breves; rami saepe stolones subterraneos tenues vix ad 1 mm. crassos emittentes. . 17. *S. stolonifera*

Folia superne haud (var. *camdensis* excepta) stomatifera; ramuli hornotini annotinique pl.m. elongati, rami ut videtur haud stoloniferi. . . . . 16. *S. ovalifolia*

[6] Of course if their exact locality is known, we shall certainly be able to determine even young male branchlets.

[7] The shape of the ventral gland is often rather variable in any species because the gland may be more or less lobate, bifid, or bipartite.

Amenta perfecte evoluta vulgo ultra 1.5 et ad 4–5 cm. longa et 1–1.3 cm. crassa, bracteis longe et dense pilosis satis sericea; folia matura majora vel tenuiora et subtus vix reticulata, juvenilia magis sericea vel sericeo-villosula, vel stipulae (saltem in ramulis vegetis) pl.m. distincte evolutae.

Folia superne haud stomatifera (var. *subcordata* excepta quae foliis amentisque maximis a *S. anglorum* valde differt) ceterum ut in p. 56 descripta; amenta 1.5–5:1.3 cm. magna; ramuli pedunculiferi vulgo 2–4 mm. crassi (confer etiam 16c. *S. ovalifoliam*, v. *subarcticam*)

15. *S. arctica*

Folia superne stomatifera, ceterum ut in p. 56 descripta; ramuli pedunculiferi 1 ad vix 2 mm. crassi (confer etiam 27. *S. anamesam* e Groenlandia) . . 14. *S. anglorum*

2. Bracteae pl.m. concolores, flavescentes et fere glabrae vel stramineae flavobrunnescentesve et pl.m. breviter sericeo-villosae (pilis quam bractea brevioribus instructae) vel subdiscolores sed tantum villosae vel pilis sericeis vulgo tenuissimis praeditae; frutices prostrati vel saepe erecti, 0.3–1 m. alti.

Amenta minima vel parva, 5–10 mm. longa vel in *niphoclada* ad 22:4 mm. magna et laxiflora; petioli vix ultra 2 mm. longi.

Folia parva, vix ad 2.5 cm. longa et ad 1.4 cm. lata, superne stomatifera, stipulae ut videtur nullae; bracteae flavescentes vel stramineae, subglabrae vel extus dense breviter pilosae; glandulae 2

21. *S. chlorolepis*

Folia saepe ad 4 cm. longa, superne haud stomatifera; stipulae vulgo evolutae; bracteae stramineae, utrinque brevipilosae; glandulae 2

20. *S. niphoclada*

Amenta 1.2–3.5 cm. longa, ultra 5 mm. crassa; petioli vulgo ultra 2 mm. longi; confer formas diversas sub 24. *S. glauca*, 25. *S. cordifolia*, et 26. *S. anamesa* enumeratas.

B. Filamenta pl.m. pilosa (interdum ima basi tantum pilis paucis instructa)

I. Amenta serotina, pseudoterminalia, anguste cylindrica vel minima pauciflora, pedunculis nudis iis saepe subaequilongis suffulta; bracteae breviter (rarius longius) pilosae, pl.m. concolores, flavescentes vel violaceae; folia satis crassa, superne saepe pl.m. inciso-reticulata, haud stomatifera, subtus distincte elevato-reticulata, pl.m. longe petiolata; glandulae 2 vel interdum plures pseudodiscum lobulatum formantes.

Bracteae intus pl.m. brevipilosae vel utrinque sericeae; folia coriacea, pleraque vix longiora quam lata vel ultra 4 cm. longa, superne conspicue inciso-reticulata, rugosa.

Frutex prostratus; folia cito glaberrima vel rarius pilis paucis sericeis obsita, vix ad 5:5.5 cm. magna et petiolis elongatis ad 3 cm. longis instructa; bracteae intus tantum brevi-pilosae; antherae violaceae..... 1. *S. reticulata*

Frutex prostratus vel erectus; folia etiam adulta subtus dense sericea vel majora, magis oblonga, margine distincte crenata, vel petioli breves gemmis vix longiores: bracteae utrinque pl.m. sericeae; antherae flavae..... 2. *S. vestita*

Bracteae glabrae vel tantum parce ciliatae; folia tenuiora, minima vel distincte longiora quam lata, vix ultra 3.5:2 cm. magna, superne vix vel indistincte inciso-reticulata; frutices prostrati, interdum minimi, suffruticulosi

4. *S. nivalis* et var. *saximontana*

II. Amenta coetanea, rarius serotina, lateralia, ovata vel cylindrica, semper multiflora, sed interdum parva, pedunculis semper foliatis.

Folia brevissime petiolata, petiolis vix ultra 2.5 mm. longis vel quam gemmae evolutae pl.m. brevioribus, ceterum ut in p. 58 indicata; amenta sub anthesi 5–10(–15):2–8(–9) mm. magna; antherae minimae, ellipsoideo-globosae

22. *S. brachycarpa*

Folia distinctius petiolata; amenta vulgo ultra 15 mm. longa, crassiora vel antherae magis ellipsoidales oblongiores et folia superne pl.m. stomatifera (specimina mascula specierum sequentium sub anthesi sine foliis perfecte evolutis accurate discernere saepe impossibile videtur; confer etiam 28. *S. lingulatam* speciem incertam alaskanam).

Folia superne pl.m. (interdum tantum sparse secundum nervos) stomatifera, vulgo oblonga, $2\frac{1}{3}$–4plo longiora quam lata, sed vix ultra 4:1.8 cm. magna.

Amenta pedunculis vix ad 1 cm. longis suffulta, 8–15:7 mm. magna, densiflora; folia pedunculorum (saltem subtus) dense breviter sericea vel villosula (confer etiam 27. *S. anamesam* e Groenlandia)....23. *S. pseudolapponum*

Amenta saepe longius pedunculata, 1.5–3.5:0.8–0.9 cm. magna et basim versus laxiflora vel folia pedunculorum etiam subtus glabra vel subglabra.....24. *S. desertorum*

Folia superne haud stomatifera, majora, latiora vel longiora.

Amenta deflorata ad fere 3.5 cm. longa, basi vulgo pl. m. laxiflora vel folia pedunculorum satis oblonga, circ. $2\frac{1}{2}$–$3\frac{1}{2}$plo longiora quam lata.....25. *S. glaucae* varietates

Amenta deflorata vulgo haud ultra 2(–2.5) cm. longa, etiam basi densiflora vel folia pedunculorum latiora brevioraque vix ad $2\frac{1}{2}$plo longiora quam lata

26. *S. cordifolia*

Enumeratio sectionum specierumque

I have omitted from the keys and the following enumeration the well known and easily recognizable *S. candida* Flügge which BALL (1909) includes in his section ARCTICAE, because I attribute to it a different systematic position.

Sect. I. RETICULATAE[8] Fries in Sylloge Pl. Nov. Soc. Ratisb. 2:38 (Consp. Disp. Salic. Suec.). 1828, quoad *S. reticulata;* for

[8] There is the older name *Chamaetia* given by DUMORTIER in Bijdr. Natuurk. Wetensch. 1:56 (Verh. Gesl. Wilgen 15) 1835 to a group, including *S. retusa*, *S. herbacea*, and *S. reticulata*. Unfortunately neither the International Rules nor the Philadelphia Code contains a precise rule in regard to the application of names of sections or similar groups. I do not accept DUMORTIER's name because in his paper he proposes two very different arrangements, and he does not in my opinion make a definite statement.

further literature see SCHNEIDER in SARGENT, Pl. Wils. **3**:146. 1916. —This section, which is represented in America by the following 4 species, is a well defined group. The rather exceptional position of *S. reticulata* among the other willows, which once led A. KERNER to propose the new genus *Chamitea* for it, becomes less marked by the addition of the American *S. nivalis;* and the characters of the RETICULATAE are further changed by the inclusion of *S. leiolepis* with glabrous ovaries. *S. glacialis* referred by RYDBERG to this section is a very imperfectly known species, of which the systematic position is still doubtful.

1. S. RETICULATA L., Sp. Pl. **2**:1018. 1753.—*S. reticulata* α *glabra* Trautvetter in LEDEB., Fl. Alt. 291. 1833.—*S. reticulata* b *normalis* And. in Öfv. K. Vet.-Akad. Förh. **15**:133 (Bidr. Känned. Nordam. Pilarter). 1858.[9]—*S. reticulata* α *typica* 1. *glabra* And. in DC., Prodr. **16**[2]:301. 1868.—This willow has the most extensive range of all the known species. In Europe it is reported from the high Pyrenees through the whole range of the Alps to the mountains of Croatia, and northward to Scotland, Scandinavia, Iceland, Spitzbergen, and Arctic Russia, while in Asia it is found on the high mountains from the Ural to Kamchatka and in the Arctic zone from Taimyr Peninsula to the Bering Strait. According to LANGE it does not occur in Greenland. In North America I have seen specimens from southern Labrador, western Newfoundland, the northern shores of the Hudson Strait, and the western shore of Hudson Bay to the Coronation Gulf and Bernard Harbor (114°46′ W. long.), and west of 135° W. long. from the Yukon Territory (King Point and Herschel Island to Lake Bennett) and from Alaska. Here it stretches, as COVILLE has said, over the Arctic zone, but including the extreme north (Camden Bay), and southward it occurs at timber line on the mountains from the Juneau region to Kodiak Island, and westward to the Aleutian, Pribilof, and St. Matthew Islands. There is also a specimen from the "Rocky Mountains" (no. 85 Herb. H.B.T., ex Herb. Torrey in N.; m., f.), the exact locality of which is unknown to me. No. 86 also

[9] The same article has been published with slight alterations in the same year in Proc. Amer. Acad. **4**: 50 (Salic. Bor.-Am.) and in Walper, Ann. Bot. **5**:744. I do not always repeat these quotations.

of the same collection is a female specimen which seems to represent a very small form of *S. reticulata* somewhat similar to *S. nivalis*, but showing a distinct reticulation of the leaves. It needs further observation and has already been mentioned by RYDBERG (1899), who also cites a specimen of MACOUN (18849, O.) from Silver City in the Rockies, a locality I have not yet been able to identify. Otherwise it is replaced in the Rockies by *S. nivalis* and var. *saximontana*.

The name *S. orbicularis* has been given by ANDERSSON (in DC., Prodr. **16**[2]:300. 1868) to the *S. reticulata* "in Kamtschatka et in America boreali-occidentali ut ad Sitchka et Unalaschka." RYDBERG (in Bull. N.Y. Bot. Gard. **1**:260. 1899) accepted this name for almost all the American material of *S. reticulata*, citing only three specimens "which may be referred" to LINNAEUS' species. But I agree with COVILLE (in Proc. Wash. Acad. Sci. **3**:342. 1901) that the distinguishing characters assigned by ANDERSSON as well as those given by RYDBERG are insufficient "to see in our American plant a species distinct from the European." If we wish to distinguish the form with more or less orbicular leaves we may use the name *S. reticulata subrotunda* Seringe (Essai Mon. Saules Suisse 29, 1815) based on *S. reticulata* Hoffmann (Hist. Salic. **1**: *pl. 25, fig. 3.* 1787). Other variations of this species which have been observed in the Old World are not represented among the American material before me and are not mentioned by previous authors.

2. S. VESTITA Pursh, Fl. Amer. Sept. **2**:610. 1814.—*S. reticulata* α *vestita* And. in Öfv. K. Vet.-Acad. Förh. **15**:133. 1858, excl. specim. e Siberia et Helvetia.—*S. vestita* α *humilior* And. in DC., Prodr. **16**[2]:300. 1868, excl. specim. altaica.—The range of this well known species extends (including the form mentioned later) in the east from northern Labrador southward to western Newfoundland, Anticosti, and the Gaspé Peninsula, and I saw it also from the west shore of Hudson Bay (Churchill, lg. *J. M. Macoun*, no. 79143, O., m., f.; Cor., G.), while in the west it reaches its northern limit in the Rockies of Alberta and British Columbia toward the 52d parallel, extending southward to northwestern Montana and the Wallowa Mountains in eastern Oregon. The western forms have been called *S. Fernaldii* by BLANKINSHIP (in Mont. Agric. Coll. Sci. Stud.

1:46. 1905), which name is adopted by RYDBERG (Fl. Rocky Mts. 198. 1917), although he says "perhaps not distinct from the eastern *S. vestita* Pursh." It certainly cannot be distinguished specifically, and if we intend to apply a special denomination to the more erect form with rather "thinner, narrower, rounded or pointed leaves," we have to use the name var. *erecta* And. (in DC., Prodr. **16**^{2}:300. 1868). The aments are usually longer than in the eastern form, but there are specimens before me from Alberta (lg. REHDER and also JACK) with the same short fruiting catkins. Professor FERNALD kindly pointed out that the shape of the capsules of typical *vestita* is more ovoid-conical, with a rather pointed apex, while it is more ovoid-ellipsoid, with an obtuser apex, in var. *erecta*. There seem to be rather intermediate forms, but as a whole this character may be taken for the best one to distinguish these eastern and western forms.

Another form has been collected by FERNALD and ST. JOHN in western Newfoundland which seems closely connected with the next species, but its description has not yet been published and it needs further observation.

3. S. LEIOLEPIS Fernald in Rhodora **16**:178. 1914.—This is a very peculiar species, which was discovered by FERNALD and ST. JOHN on the Table Mountain, Port à Port Bay, in western Newfoundland, July 17, 1914, on "mossy knolls on the limestone tableland, alt. 200–300 m." (no. 10825, fr.; G.). In habit and foliage it closely simulates, as the author said, *S. reticulata* and the most dwarfed alpine extreme of *S. vestita;* but it differs "from both in the glabrous scales and capsules; also from *S. reticulata* in its short peduncles and thick fruiting aments, and from *S. vestita*, which is the most abundant willow of Table Mountain, in its glabrous or quickly glabrate foliage and the smaller and more slender, glabrous, greenish terminal buds." As the type specimen shows, the ovaries are sometimes sparsely pubescent, the bracts frequently provided with a few cilia, the styles very short but more or less distinct, and even the old leaves bear some hairs on the lower surface which are often rather difficult to recognize. Unfortunately the male sex is still unknown; consequently I cannot decide whether *S. leiolepis* is to be regarded as a good species or as a glabrate variety of *S. vestita*,

representing a rather dwarfed alpine form. The glabrousness or pubescence of the ovaries, a character on which usually so much reliance is placed, cannot always be taken for a decisive taxonomic character. In my notes on the species of the section OVALIFOLIAE (*l.c.*) I was able to show that many species with hairy ovaries develop a more or less glabrescent or glabrous variety, or vice versa.

4. S. NIVALIS Hooker, Fl. Bor.-Am. **2**:152. 1839; Nuttall, N. Am. Sylva **1**:77. *pl. 19, fig.* sinistra inferior. 1843; Rydberg in Bull. N.Y. Bot. Gard. **1**:262. 1899; Ball in Coult. and Nels., New Man. Rocky Mt. Bot. 139. 1909.—*S. reticulata* c *nana* And. in Öfv. K. Vet.-Akad. Förh. **15**:133. 1858, excl. specim. e Groenl. et Spitzb.—*S. reticulata β nivalis* And. in DC., Prodr. **16**^{2}:301. 1868.—The type of this "elegant and very diminutive shrub" (NUTTALL) was collected "near the summits of the peaks in the Rocky Mountains" by DRUMMOND between lat. 52–56°. It occurs most frequently in the alpine region of the Rockies of Alberta and British Columbia, and to a certain degree also on the Tobacco Root Range (Pony Mountains), on Observation Mountain and Mt. Chauvet in southern Montana, and on the Electric Peak in northern Yellowstone Park. It is also mentioned by PIPER from Mt. Rainier, Washington. There are a few specimens from Colorado (*E. L. Greene*, no. 517, m.; G.; probably from near Golden City) and from southeastern Utah (*Rydberg* and *Garrett*, no. 8787, m., f.; N.; La Sal Mts., West Mt. Peale) which I can hardly distinguish from typical *S. nivalis*, and which, in my opinion, form connecting links between it and *S. saximontana* Rydbg. I take this last species, therefore, only for a variety of *S. nivalis*, from which it chiefly differs by the characters given later. RYDBERG himself said (1899) that *S. nivalis* "perhaps represents only the most depauperate form" of his *S. saximontana*, and he repeats in his Cat. Fl. Mont. 112. 1900 that the latter "seems to grade into *S. nivalis*," while such an accurate observer as PIPER (in Contr. U.S. Nat. Herb. **9**:216. 1906) states that "*S. saximontana* probably is not specifically distinct from *S. nivalis*."

4b. S. NIVALIS var. **saximontana,** nov. var.—*S. reticulata* Bebb in Coulter, Man. Rocky Mt. Bot. 339. 1885, non L.; Ball in Trans. St. Louis Acad. Sci. **9**:90. 1899.—*S. saximontana* Rydberg in Bull.

N.Y. Bot. Gard. 1:261. 1899; Ball in Coult. and Nels., New Man. Rocky Mt. Bot. 139. 1909.—*S. aemulans* v. Seemen in Bot. Jahrb. 29: Beibl. 65:28. 1900.—A typo praecipue differt: ramis crassioribus (interdum ad 19 mm. crassis), foliis majoribus vulgo 1.5–3.5 cm. longis et 0.8–2 cm. latis interdum minus reticulatis forma ut in typo valde variabilibus (lanceolatis saepe apice subacutis), petiolis ad 1.8 cm. longis; amentis pluri- vel multifloris masculis 7–12 mm. longis pedunculis vulgo longioribus sparse pilosis exclusis, femineis 8–18 mm. longis fructiferis fere ad 1 cm. crassis.

The type came from Gray's Peak in Colorado (lg. RYDBERG, August 1895, m.; N.), and it is most abundant in the Rockies of this state, reaching its southernmost point on the Truchas Peak of the Taos Mountains in northern New Mexico. Northward its range extends through western Wyoming, Yellowstone Park, and southern Montana to the vicinity of Laggan in Alberta and Skagit Valley in British Columbia, while toward the west it is found on Mt. Rainier in Washington, on the Strawberry and the higher Wallowa Mountains in eastern Oregon, furthermore on the East Humboldt Mountains in northeastern Nevada, and also in Boxelder and Utah counties and on the La Sal Mountains in Utah.

Sect. 2. HERBACEAE Borrer in Hooker, Brit. Fl. 432. 1830 (Sect. CHAMAETIA Dumortier, pro parte, see note 8 on p. 43; sect. RETUSAE Kerner in Verh. Zool. Bot. Ges. 10:195 [Niederöstr. Weid.]. 1860; for further literature see SCHNEIDER in Sargent, Pl. Wils. 3:142. 1916).—As I have already explained (*l.c.* 143), it seems to me impossible to separate the sect. RETUSAE from the HERBACEAE, but there are the following species which have been added to this group or might be regarded as closely related to its members: *S. cascadensis*, *S. Dodgeana*, *S. glacialis*, *S. Peasei*, *S. polaris*, *S. phlebophylla*, *S. rotundifolia*, and *S. Uva-ursi*. Of these species *S. rotundifolia* seems to show the most intimate affinity with *S. herbacea*, but it is distinguished by the persistent leaves, a character also found in *S. phlebophylla*, *S. cascadensis*, and *S. Uva-ursi*. From the last three species *S. Uva-ursi* seems to be widely separated by its bicolor leaves and the single stamen of the male flowers, while on the other hand they all have bicolor or fuscous bracts which are concolor, greenish or yellowish (or partly purplish

toward the apex) in *S. herbacea*, *S. Dodgeana*, and *S. retusa*. The systematic position of *S. polaris* is even more puzzling. Some authors are inclined to regard it as nothing but a variety of *S. herbacea* because the vegetative characters of both are so similar; but if we base our opinion on the flowers we may come to a very different conclusion; and in Sargent, *l.c.* 319, I have included this species in the sect. MYRSINITES Borrer. If we pay much attention to the presence or absence of a dorsal gland in the male flowers, we might also refer *S. Uva-ursi* to this section, but this willow occupies a rather unique position among the American species. With my present knowledge I deem it best to leave the question of the correct limitation of this section and of the true systematic position of these species undecided until I have had opportunity to discuss this problem with such an eminent salicologist as S. J. ENANDER, who is preparing a monograph of the whole genus. I have already published (Oestr. Bot. Zeitschr. **65**:273. 1915) a short note on the systematic arrangement of the genus and discussed briefly the views taken by ANDERSSON and VON SEEMEN. The main purpose of that note was to show that no systematic grouping on natural lines can be attained unless we make use of every taxonomic character.

5. S. POLARIS Wahlenberg, Fl. Lapp. 261. *pl. 13. fig. 1.* 1812; Rydberg in Bull. N.Y. Bot. Gard. **1**:264. 1809; Coville in Proc. Wash. Acad. Sci. **3**:335. *fig. 27.* 1901.—? *S. herbacea* var. *polaris* Kurtz in Bot. Jahrb. **19**:475. 1894.—In America this species is only known from the Alaskan coast of Bering Strait, where it has been collected at Port Clarence and Cape Vancouver. I have seen only the Port Clarence specimens of *Trelease* and *Saunders* (nos. 3387, f., 3385[a], m.), which have been described by COVILLE. They seem to agree with specimens of S. J. ENANDER'S Salic. Scand. Exsicc. from Spitzbergen, especially with no. 12 "modificatio foliis subovalibus." The ovaries of no. 3387 are partly glabrate, and I cannot at present say whether the American *S. polaris* is the typical form or not. As to its uncertain systematic position see my preceding remarks.

LUNDSTRÖM (apud KJELLMAN in Nordenskjöld, Vega Exp. Vet. Iakt. **2**:21 [Fanerog.-Fl. St. Lawrence-Ön.]. 1883) has described a *S. polaris* f. *subarctica* "foliis tenuioribus, subtus margineque pilis

longis parce adspersis, squamis atris, obtusis; stylo elongato," the type of which was collected by KJELLMAN, July 31 to August 1, 1879, on the northwestern shore of St. Lawrence Island. I cannot interpret this form without having seen the type, and it is not mentioned by COVILLE or RYDBERG. There is, however, a specimen before me collected by *R. L. Shainwald, Jr.*, on Mt. McKinley, 1200 m., August 26, 1903 (fr.; N.), which is very similar to *S. polaris* in every respect, but the fruiting aments measure up to 3 cm. in length and 9 mm. in width. The sessile fruits are 5–6 mm. long, pubescent only toward the apex, and the distinct withered style is a little longer than the stigmas. It looks to me like a new variety of *S. polaris* or a new species.

6. S. UVA-URSI Pursh, Fl. Amer. Sept. **2**:610. 1814; Rydberg in Bull. N.Y. Bot. Gard. **1**:278. 1899; Britton and Brown, Ill. Fl. **1**:601. *fig. 1477*. 1913; Robinson and Fernald, Gray's New Man. 325. *fig. 656*. 1908.—*S. Cutleri* Tuckerman in Amer. Jour. Sci. **45**:36. 1843; And. in Öfv. K. Vet.-Akad. Förh. **15**:132. 1858; in DC., Prodr. **16²**:292. 1868.—*S. Myrsinites* var. *parvifolia* Lange, Consp. Fl. Groenl. **1**:108. 1880; **2**:278. 1887; Fl. Dan. **17**:fasc. 51:13. *pl. 3053*. 1883, non And.—*S. ivigtutiana* Lundström apud Berlin in Öfv. K. Vet.-Akad. Förh. **41**:89. 1884.—A well known willow, of which, however, as I said before, the systematic position is by no means settled. ANDERSSON said, "A *S. arbuscula* recedit foliis minimis parte superiore serrulatis, amentis subterminalibus et capsulis glaberrimis. Longius a *S. retusa* distat. Si ut ferunt auctores americani, flores masculi staminibus tantum singulis praediti sunt, tum affinitas cum *S. coesia* esset, cui etiam rigiditate et glaucescentia foliorum non absimilis, sed folia subserrata et capsulae glabrae." I have very rarely found two stamens in one flower, and I am at present unable to give a precise opinion as to the real relationship of this peculiar species. Its range stretches from New York (Mt. Marcy and Mt. Whiteface), Vermont (Camel's Hump, Mt. Mansfield), New Hampshire (White Mts.), and Maine (Mt. Katahdin) northward to the Gaspé Peninsula, southern and western Newfoundland and the whole coast of Labrador, apparently reaching the northern limit of its range at the southern shore of Baffinsland. Westward it extends through Ungava to the eastern

shores of Hudson Bay. The species has also been reported from southwestern Greenland by DURAND (in Jour. Acad. Nat. Sci. Phil. II. 3:197 [Pl. Kaneanae Groenl.] 1856), but LANGE (Consp. Fl. Groenl. 1:108. 1880) made the following statement: "*S. Uva Ursi* Durand ex descriptione (Pl. Kan.) ad formam nostram 3 [*S. arctophila lejocarpa*] retuli, etsi specimina Kaneana non vidi, quare dijudicare nequeo, an forsan ad veram *S. Uva Ursi* Pursh . . . . pertineant, species, quae tamen a nemine alioquin in Groenlandia lecta esse constat." I am inclined to believe that KANE's specimens represented the true *S. Uva-ursi*, because this species is apparently identical with *S. Myrsinites parvifolia* Lange and *S. ivigtutiana* Lundstr. LANGE said that he did not see specimens of the typical *S. Myrsinites* L. from Greenland, and his var. *parvifolia* seems to be distributed from about the 70th parallel to the very south in Greenland. I have seen one specimen from the Tunugdliarfik Fjord, Kingua, lg. *L. K. Rosenvinge*, August 17, 1888 (fr.; G.), which fully agrees with LANGE's and LUNDSTRÖM's descriptions, and, in my opinion, cannot be separated from *S. Uva-ursi*, the presence of which may be expected in this part of Greenland. The leaves are distinctly glaucous beneath, while they are green and shining on both sides in *S. Myrsinites*. ANDERSSON's var. *labradorica* (1868) from near Oakak on Labrador is scarcely different from the type. He based it on *Hohenacker's* no. 92[c], which I have not yet seen. On the other hand, the forms referred to *S. Uva-ursi* by HOOKER (Fl. Bor.-Am. 2:152. 1839) seem to belong at least partly to *S. arctophila*, but I have as yet seen only a few leaves of *Morrison's* specimen in Herb. Bebb in C. which do not have stomata in the upper epidermis, as is always the case in PURSH's species.

7. S. PEASEI Fernald in Rhodora 19:223. 1917.—This willow is known only from the type locality in New Hampshire, southwest gully of King's Ravine on Mt. Washington, where it was first collected by *Pease* (no. 12091; the type is *Fernald* and *Pease*, no. 16847, fr.; G.). It is certainly a very peculiar species, and needs further observation, the male plant being still unknown. FERNALD's description is, as usual, ample and fitting. I am almost sure that it has to be regarded as of hybrid origin. I visited King's Ravine on September 18, 1918, and I found the willow growing in

about the altitude given by FERNALD on wet cliffs in company with *S. herbacea*. The main part of *S. Peasei* I saw was growing about 15–30 m. below *S. herbacea* on the southern slope of the ravine and covered a rather large area. *S. Uva-ursi* is very common at a somewhat higher level, but I collected plants of it which were growing just above the place where I saw *S. herbacea* and *S. Peasei* close together. Some plants of *S. Peasei* looked much like vigorous *S. herbacea*, while the main part of it lower down at first sight could easily be taken for *S. Uva-ursi*. FERNALD states that *S. Peasei* "finds itself at home on the almost inaccessible wet cliffs," and perhaps he did collect it somewhere else (but apparently not far from where I found it), because this place is by no means "almost inaccessible." Anyone who is a little careful not to start a stone avalanche and is not afraid of some steep climbing can easily visit this locality. Unfortunately the weather became misty and prevented my exploring the southwestern part of the ravine to a greater extent. On the southeastern slopes (toward the Madison Huts) I could not find a trace of either *S. herbacea* or *S. Peasei*, both species seeming to inhabit a very limited area. Under the lens the leaves, above as well as beneath, look as though very finely punctate owing to the presence of stomata. They are not "papillose," as the author says. These stomata are also present in *S. Uva-ursi*, but usually hardly visible except under the microscope.

8. S. HERBACEA L., Sp. Pl. **2**:1918. 1753; Lange, Consp. Fl. Groenl. **1**:107. 1880; **2**:278. 1887; Rydberg in Bull. N.Y. Bot. Gard. **1**:277. 1899; Robinson and Fernald, Gray's New Man. 325. *fig. 65*. 1908; Britton and Brown, Ill. Fl. ed. 2. **1**:601. *fig. 1478*. 1913.—It has almost exactly the same range as *S. Uva-ursi;* it does not occur, however, in New York and Vermont, and I have not seen specimens from Newfoundland. On the other hand, it is met with on the western shores of Hudson Bay and in western as well as eastern Greenland. It is entirely absent from western North America, but in Europe and Asia its range is even more extensive than that of *S. reticulata*. PURSH (Fl. Am. Sept. **2**:617. 1814) cites a specimen of *D. Nelson* from "the northwest coast" which I cannot identify.

9. S. ROTUNDIFOLIA Trautvetter in Nouv. Mem. Soc. Imp. Nat. Mosc. **2**:304. *pl. 11* (De Salic. Frig. Kochii). 1832; Andersson in DC., Prodr. **16**²:299. 1868; Rydberg in Bull. N.Y. Bot. Gard. **1**:276. 1899; Wolf[10] in Izv. S.-Petersburg Liesn. Inst. **5**:112. *pl. 38. fig. 15–20. pl. 46. fig. 7–9.* 1900.—*S. polaris* var. *leiocarpa* Chamisso in Linnaea **6**:542. 1831.—*S. retusa* var. *rotundifolia* Treviranus ex Trautv. in Nouv. Mem. *l.c.*, pro synon.; Trautvetter in Middendorff, Reise Sib. 1. pt. 2. Bot. Abt. **1**:152 (Fl. Boganid. Phaen.) 1847.—*S. rotundifolia α typica* Lundström in Nov. Act. S. Sci. Ups. ser. 3. 1877. 30. *fig. 3.*—*S. leiocarpa* Coville in Proc. Wash. Acad. Sci. **3**:338. *pl. 41. fig. 2.* 1901.—"This charming little plant . . . . grows on the islands and both shores of Bering Sea and the Arctic Ocean, and above timber line on the Pacific coast of Alaska eastward to Prince William Sound," and to these localities given by COVILLE is to be added Collinson Point on Camden Bay, where it was collected by *F. Johansen*, June 13, 1914 (no. 39 or 93811 O., m.). The typical form has glabrous ovaries, but two of the specimens before me represent a form with more or less hairy ovaries which I deem best to keep distinct as

f. **pilosiuscula,** f. nov. (ab typo ut videtur nonnisi ovariis partim vel omnino villosis differt). As type may be taken no. 3382 of *Trelease* and *Saunders*, from Hall Island, July 14, 1809 (f.; M.), to which no. 3383 from Matthews Island, July 15 (f.; M.), is to be added. The last specimen has a little longer styles with more or less slender stigmas, thus somewhat resembling *S. stolonifera*, but otherwise not differing from *S. rotundifolia*.

10. S. PHLEBOPHYLLA Andersson in DC., Prodr. **16**²:290. 1868; Coville in Proc. Wash. Acad. Sci. **3**:336. *fig. 28.* 1901.—*S. anglorum* Chamisso in Linnaea **6**:541. 1831, pro parte, quoad specimin. citata; Trautvetter in Act. Hort. Petrop. **6**:37. 1879.—*S. buxifolia* Trev. apud Trautv. in Nouv. Mem. Soc. Imp. Nat. Mosc. **2**:301. *pl. 10.* 1832,

[10] WOLF, one of our best salicologists, who was curator of the Imperial Institute of Forestry at Petrograd, at least until the outbreak of the war, has made some extremely valuable studies on European and Asiatic willows. Unfortunately his papers are written in Russian, but they are accompanied by excellent sketches. The title of his main paper is (translated) "Materials toward the study of the willows native to European Russia," which appeared in two parts in 1900 in vols. 4 and 5 of the periodical quoted.

non Willd. apud SCHLEICHER.[11]—*S. retusa* Hooker and Arnott, Bot. Beech. Voy. 130. 1832, non L.—*S. arctica β minor* Ledeb., Fl. Ross. 3:619. 1849–51.—*S.* (*retusa*) *phlebophylla* And. in Öfv. K. Vet.-Akad. Förh. 15:131. 1858, pro parte maxima.—*S. arctica β buxifolia* [recte *minor*] Ledeb. ex And. in DC., *l.c.* 290, pro synon.—*S. palaeoneura* Rydbg. in Bull. N.Y. Bot. Gard. 1:267. 1899.—The history of this peculiar willow, which had been thoroughly described by TRAUTVETTER, is well given by COVILLE. ANDERSSON'S "species" is always quoted from 1858, but at this time he published the name *phlebophylla* only as a varietal designation, distinguishing 3 forms: *major*, *media*, and *minor*, which he rightly omitted in 1868. I saw a photograph and fragments of all his types preserved in Herb K. The f. *minor* may be represented by a specimen like *Turner's* no. 1293 in part (f.; G.), collected in 1879 on Atka Island. TURNER (Contr. Nat. Hist. Alaska 75. 1886) mentions a *S. rotundifolia* var. *retusa* from Atka Island, "with its heads of cottony catkins peering just above the surface of the other vegetation." I am not quite sure whether he refers to the form before me or not. RYDBERG has mentioned the specimen which I have seen under *S. Dodgeana*, but the leaves do not show the finely impressed veins on the upper surfaces, and the female flowers are very similar to those of *S. phlebophylla*, having, however, a dorsal gland. This form needs further observation, and the species has not yet been recorded so far south in Alaska, where it inhabits the northwestern and northern coast from Norton Sound to Point Barrow. According to COVILLE it was also collected on the Porcupine River by *Turner* in 1891, and SEEMANN (Bot. Voy. Herald 40. 1852) reported it from Pelly's Island at the mouth of the Mackenzie River. On the Siberian coast of Bering Strait *C. Wright* collected it on Arakam (or Kayne) Island. I have also seen a specimen from near Glacier in southeastern Alaska collected in June 1914 by *Mary Milvain* (m., f.; A.).

11. S. DODGEANA Rydbg. in Bull. N.Y. Bot. Gard. 1:277. 1899; Fl. Rocky Mts. 195. 1917; Ball in Coult. and Nels., New Man.

[11] According to SERINGE, Essai Mon. Saules Suisse 54. 1815, the name *S. buxifolia* Willd. was used first by SCHLEICHER, Cat. Sal. 1. 1809, where it is a nomen nudum, as well as in ed. 3 of SCHLEICHER'S Cat. Pl. Helv. 25. 1815. This name has to be used, so far as I understand it, for the hybrid *S. glauca*×*S. reticulata;* see BRAND in Koch's Syn. D. Schw. Fl. ed. 3. 3:2357. 1907.

Rocky Mt. Bot. 131. 1909.—This delicate suffruticose species is only known from the type locality, Electric Peak, in the northeast corner of Yellowstone Park (lg. *Rydberg* and *Bessey*, August 18, 1897, f.; N.) and from Sheep Mountain in the Teton Forest Reserve, Wyoming (*F. Tweedy*, no. 292, fr.; N.). RYDBERG calls it "the smallest willow in existence," but there are similar minims among the European (*S. serpyllifolia* Scop.) and Himalayan species (*S. oreophila* var. *secta* And.); see SCHNEIDER in SARGENT, Pl. Wils. 3:146. 1916. The systematic position of *S. Dodgeana* is not yet quite understood; it seems to represent a rather singular type among its American congeners. As to a doubtful pubescent variety, see my remarks under the following species.

12. S. CASCADENSIS Cockerell in Muhlenb. 3:9. 1907; Rydberg, Fl. Rocky Mts. 198. 1917.—*S. tenera* And. in DC., Prodr. 16²:288. 1868, non A. Braun (1850); Rydberg in Bull. N.Y. Bot. Gard. 1:269. 1901; Piper in Contr. U.S.N. Herb. 11:216 (Fl. State Wash.). 1906; Ball in Coult. and Nels., New Man. Rocky Mt. Bot. 136. 1909; in Piper and Beattie, Fl. Northwest Coast 117. 1915; Jepson, Fl. Calif. 344. 1909, pro parte.—*S. phlebophylla* Watson in U.S. Geol. Sur. Expl. 40th parallel King's Rep. 5:Bot. 326. 1871, pro parte, non And.—*S. arctica* var. *petraea* Bebb in Watson, Bot. Calif. 2:90. 1879, pro parte, non And.; Ball in Trans. Acad. St. Louis 9:89. 1899, pro parte.—*S. Brownii* var. *petraea* Bebb in BOT. GAZ. 16:107. 1891, pro parte.—*S. Brownii* var. *tenera* Jones, The Willow Fam. 19. 1908.—This species has always been regarded as most closely related to *S. petrophila*, and BALL (1899) mentioned it in the synonymy only as "a narrow-leaved form," while he (1909) says "perhaps only a variety of the preceding" (*S. petrophila*). By a close study of the material before me I have the impression, however, that it possibly might have a more intimate affinity to *S. phlebophylla*. Both BALL and RYDBERG distinguish *S. cascadensis* from *S. petrophila* only by the smaller size of the leaves and the few-flowered aments, and neither author mentions the fact that the old leaves are more or less persistent, a character not observed by me in *S. petrophila*. The leaves of *S. cascadensis* are occasionally up to 18 mm. long, and in male specimens, like no. 1074 of *Merrill* and *Wilcox* from the Teton Mountains, Wyoming, the catkins bear

more than 20 flowers, and some fruiting aments before me measure up to 2.5:0.9 cm. The systematic position of the species needs further study, however, and it is interesting to note the singular view expressed by ANDERSSON himself as to the relationship of his *S. tenera:* "Memorabilis forma a nostris *S. retusa*, *reticulata*, et *arbuscula* quasi composita. *S. retusae* similis: foliis lingulatis, vix $\frac{3}{4}$ poll. longis, supra medium 2 lin. latis, parallelo-nervosis, integerrimis; *S. reticulatae:* capsulis sessilibus, dense lanatis, pusillis; et *S. arbusculae:* amentis ramulos laterales terminalibus."

The type of *S. cascadensis* was collected by LYALL in 1860 on the "eastern summits of Cascade Mountains" (f.; K.), and LYALL'S specimens were sent out from Kew under the name *S. phlebophylla;* therefore BEBB (in BOT. GAZ. **16**:107. 1891) accused ANDERSSON rather unjustly of the use of this name for LYALL'S plant. There is no proof that ANDERSSON himself applied his own name *phlebophylla* to this form which he (1868) made the type of *S. tenera.* The writing on the labels of LYALL'S specimens is not in ANDERSSON'S hand. The specimen collected by WATSON in the Uinta Mountains, Utah (no. 1101, f.; G.), which the collector referred to *S. phlebophylla* because it seemed to match perfectly LYALL'S plant, is of peculiar interest; it looks to me more like a pubescent form of *S. Dodgeana* than anything else, but I do not venture at present to pass final judgment upon it.

Sect. III. OVALIFOLIAE Rydberg in Bull. N.Y. Bot. Gard. 1:274. 1899, pro parte, sed sensu emend.—Sect. ARCTICAE Rydbg., *l.c.* 263, pro parte, non And.; Ball in Coult. and Nels., New Man. Rocky Mt. Bot. 135. 1909, pro parte.—Sect. DIPLODICTYAE Schneider in Sargent, Pl. Wils. **3**:136. 1916.—See my first note (BOT. GAZ. **66**:117. 1918). To this section belong the following species I have dealt with (*l.c.*): 13. *S. petrophila* Rydbg., 14. *S. anglorum* Cham., 15. *S. arctica* Pall., 16. *S. ovalifolia* Trvt., 17. *S. stolonifera* Cov., and 18. *S. groenlandica* Ldstr. I wish to add some notes to the following species.

15. S. ARCTICA Pall.—Since I wrote the first article I have seen specimens (*Evans*, no. 439, partim; W.) from Kodiak which represent TRAUTVETTER'S *S. diplodictya* mentioned *l.c.* 123. It is nothing but a mere form with "foliis utrinque concoloribus."

17. S. STOLONIFERA Coville.—I mentioned (*l.c.* 137) a new f. *subpilosa* of which as type may be taken B. E. FERNOW's specimen from Glacier Bay, Point Gustavus, June 10, 1899 (Cor.). There are specimens before me from the same bay, Muir Glacier, collected between June 8 and 12, 1899, by *F. V. Coville* and *T. H. Kearney* (no. 621, f.; W.). COVILLE is of the opinion that they, at least partly, represent a hybrid between *S. arctica* and *S. stolonifera*. One of the sheets (no. 373447, W.) looks indeed like such a hybrid; the leaves seem not to possess stomata in the upper epidermis and are partly larger, while the flowering aments measure up to 3:1 cm. The other specimen (of sheet no. 376920), however, can hardly be separated from *S. stolonifera* except by the tomentose ovaries. The leaves have numerous stomata in the upper epidermis, are of the usual size and shape, and the aments are not larger than in typical *stolonifera*. This specimen looks to me more like f. *subpilosa* than like a hybrid. It may be, however, that we have to take all the specimens with more or less pubescent ovaries and fruits for those of hybrid origin, but this does not seem likely to me.

18. S. ARCTOPHILA Cock.—Professor T. D. A. COCKERELL kindly informed me that he had published in the last edition of HELLER's Cat. N. Am. Pl. p. 89, 1910, this new name for *S. groenlandica* Lundström but not of Heer (Fl. Foss. Arct. 1:101. *pl. 4. figs. 8–10.* 1868). I was not aware of this fact, neither had I seen the sheets of this edition of HELLER's Catalogue. Besides, COCKERELL's name is not found in the card index published by the Gray Herbarium. I accept this new name, but there is no definite statement in the international rules as to the priority of names of paleontological plants. Owing to this change I have to propose the following new combination, *S. arctophila* var. **lejocarpa** for *S. groenlandica* var. *lejocarpa* Lange (*l.c.* 141).

18a. **S. hudsonensis,** spec. nov.—*S. fullertonensis*×*S. groenlandica* Schneider in BOT. GAZ. **66**:342. 1918.—Frutex prostratus habitu *S. arctophilae*, ramis pl.m. subterraneis radicantibus ad 5 mm. crassis, ramulis elongatis repentibus glabris ut in *S. arctophila* coloratis, gemmis foliisque ut l.c. a me descriptis sed gemmis interdum ad 9 mm. longis et foliis angustioribus acutioribus ad 3.5:1.7 cm. latioribus ad 3.5:2 cm. magnis superne vulgo haud stomatiferis

maturis glabris vel utrinque sparse pilosis; amentis tantum fructiferis visis 2: 1.3 ad 4: 1 cm. magnis ramulos foliatos ad 4 cm. longos terminantibus; fructibus ad 9 mm. longis pedicello brevissimo vel glandula vulgo distincte breviore excluso.

Besides the specimens mentioned (*l.c.* 342), I examined the following: Hudson Bay: 50 miles south of Cape Eskimo, August 5, 1900, *E. A.* and *A. E. Preble* (no. 43, fr., type, 46, st.; W.); 25 miles south of Cape Eskimo, August 12, 1900, same coll. (nos. 54, 57, fr.; W.).

After having seen the material collected by the PREBLES I think it best to propose a new name for this interesting form, which after all seems to represent a new species closely related to *S. arctophila*, from which it chiefly differs in the shorter pedicels and the more elongated gland. Judging by the flowers alone, one might be inclined to take it for a form of *S. anglorum*, but the leaves are mostly without any trace of stomata in the upper epidermis, and their color and texture are more like in *S. arctophila*. Some specimens cited in my second note may represent hybrids between this species and *S. fullertonensis*. Unfortunately I have not yet seen young female or male flowers, and further investigation is needed to elucidate the real affinity of this form, which seems to be fairly common along the western shores of Hudson Bay from James Bay to Cape Fullerton and also on the islands in the western part of Hudson Strait.

Sect. IV. GLAUCAE E. Fries, Syllog. Pl. Nov. 2:36. 1828, pro parte.—Sect. ARCTICAE Rydbg. in Bull. *l.c.* pro parte; Ball in Coult. and Nels, *l.c.*, pro parte. For further synonymy see SCHNEIDER in Sargent *l.c.* 147. 1916.—In my second paper (BOT. GAZ. **66**:318. 1918) I have already explained the differences between this section and the ARCTICAE, and there I have also discussed the following species, which are to be referred to this section: 19. *S. fullertonensis* Schn., 20. *S. niphoclada* Rydbg., 21. *S. chlorolepis* Fern., 22. *S. brachycarpa* Nutt., 23. *S. pseudolapponum* v. Seem., 24. *S. desertorum* Rich., 25. *S. glauca* L., 26. *S. cordifolia* Pursh, 27. *S. anamesa* Schn., and 28. *S. lingulata* And.

I wish to add the following remarks, because I had the opportunity to study some very interesting material of Herb. W., and I

desire to express my gratitude to the curator of the U.S. Nat. Herbarium.

20. S. NIPHOCLADA Rydbg.—Having seen a co-type and other material of this species from Herb. W., I wish to correct my statements (*l.c.* 339) as follows: The co-type collected by *Miss E. Taylor* has ripe fruits which measure up to 7 mm. in length and show a distinct pedicel (about 1.3 mm. long) which is distinctly longer than the bifid gland. The male type described by COVILLE (*Funston*, no. 185) has short aments measuring about 10:4–5 mm. and loosely flowered at the base, but there is a specimen collected by *F. C. Schrader* on the John River in northern Alaska, July 10, 1901, of which the female part well agrees with the type of *S. niphoclada*, while the male aments measure up to 22:4 mm., being very slender and loosely flowered. In FUNSTON's specimens the male flowers are younger, but I hardly believe that they could grow to the size of those of SCHRADER's plant. Otherwise the flowers are identical, having glabrous filaments and ventral glands of a similar shape. SCHRADER, however, collected another male specimen on Anaktuvuk River (erroneously spelled Ansktoobah River on the label) August 5, 1901, of which the aments are like those of the John River plant, but the filaments are somewhat hairy at base. Otherwise I cannot separate SCHRADER's plants, and I believe that the pubescence of the filaments which mostly can be taken for a constant character may not be of reliable taxonomic value in this case. We need, of course, a better acquaintance with all the willows of this region to decide the question whether or not the absence or presence of a pubescence on the filaments is a really important character. A fruiting specimen collected by SCHRADER at the same place and date as the last mentioned male one seems to me inseparable from *S. niphoclada*, but the ripe fruits measure up to 8 mm. in length, are almost sessile, and of a more ovoid-conical shape than in the type.

The specimen mentioned (*l.c.* 339) from Fort Churchill, Hudson Bay, collected by *E. A.* and *A. E. Preble*, is really no. 41, not no. 26 (as given by me and by COVILLE), according to a note by E. A. PREBLE on the sheet (no. 385093) in Herb. W. From the same place the same collectors brought a male specimen (no. 33; W.) which I refer to *S. brachycarpa*, which had been collected there

also by *F. M. Macoun* (*l.c.* 337). PREBLE'S no. 41 may be more closely connected with *S. brachycarpa* than with *S. niphoclada*, but the shape of most of the larger leaves is more elongate-lanceolate in no. 41, where the largest leaves measure up to 4.5:1 cm., while those of MACOUN'S female plant are shorter and broader, and its pubescence is more like in typical *S. brachycarpa*. In no. 41 the young twigs bear a very thick villose pubescence of long soft hairs, which is far more conspicuous than the tomentum of the forms of *S. niphoclada* from the west. After all, I am inclined to believe that no. 41 may represent a form of *S. brachycarpa* comparable to f. *poliophylla* of *S. glauca acutifolia*. We must not forget, however, that we hardly can elucidate those forms without a full understanding of the true *S. desertorum* (see *l.c.* 331).

I have thought it best to treat those forms at a considerable length, because we know so little of the willows of the Northwest Territories, and I wish to give an impulse to their closer investigation in the field by future collectors.

21. S. CHLOROLEPIS Fern.—I have described (*l.c.* 339) the var. *antimima*, which looks rather intermediate between the type and *S. brachycarpa*, and which on Mt. Albert seems to be connected by hybrids with the latter. There is a small male specimen in Herb. N. collected by *A. P. Low*, north of Cape Jones on the eastern coast of Hudson Bay, July 16, 1898 (no. 63272 O.). It agrees well with *S. brachycarpa*, and has hairy filaments, but I found some stomata in the upper leaf epidermis. We need much more copious material (male and female) from this locality to judge the form properly.

25. S. GLAUCA var. ACUTIFOLIA (Hook.) Schn.[12]—Having received, as already stated, very interesting material from Herb. W., I wish to add the following remarks.[13] There are before me several

[12] I stated (*l.c.* 321) that 2 *S. villosa* had been published before HOOKER described the present form under this name, but there is still a much older *S. villosa* Hoffmann (Obs. Bot. 15. 1787) which is not registered in the Kew Index, nor can I find this name mentioned by KOCH, FRIES, WIMMER, ANDERSSON, or v. SEEMEN. It was sent from Sweden by THUNBERG.

[13] In the note (*l.c.* 321) I made an entirely wrong statement in regard to PURSH'S Canadian collections. Relying on facts given by HARSHBERGER, which he in his turn took from an article in BOT. GAZ. 7:142. 1882, I said that PURSH did not collect in Canada. Professor N. L. FERNALD kindly directed my attention to PENHALLOW'S

specimens collected at Great Slave Lake, Mackenzie, which, in my opinion, are most closely related to var. *acutifolia*, but at least some of them seem to represent a very villose form of it, for which I propose the name: S. GLAUCA var. ACUTIFOLIA f. **poliophylla,**[14] forma nov.—A typo nonnisi differre videtur ramis annotinis densius villoso-lanuginosis etiam vetustioribus tomento lanuginoso pl.m. obtectis, foliis superne pl.m. laxe adpresse sericeo-lanuginosis subtus villo densissimo molli pl.m. adpresso albo vestitis. The type is Great Slave Lake, Fort Rae, July 28, 1901, *E. A.* and *A. E. Preble* (no. 139, fr.; W.; folia inferiora elliptica vel oblongo-elliptica, utrinque acuta, superiora magis ovato-elliptica apice acutiora, maxima ad 5:2.2 cm. magna; amenta fructifera pedunculo foliato ad 3 cm. longo excluso ad 5:1.3 cm. magna; fructus e basi rhomboideo ovoideo-conici, ad 9 mm. longi pedicello ad 1.5 mm. longo glandulam subduplo superante excluso).

The following specimens seem to me rather intermediate between f. *poliophylla* and typical var. *acutifolia:* Great Slave Lake: Fort Resolution, July 14, 1901, *E. A.* and *A. E. Preble* (no. 141, fr.; W.; forma minus dense quam no. 139 villosa); June 21, 1903, *E. A. Preble* (no. 194, f.; W.; eadem forma ut videtur ac praecedens sed juvenilis); Fort Good Hope, on the Mackenzie River, June 23, 1904, *E. A. Preble* (nos. 330, f. et fr. anni praeteriti, 332, f.; W.; forma a cl. RYDBERG ad *S. niphocladam* relata foliis floribus juvenilibus; sed folia distincte petiolata et fructus adulti magni). There are two other male specimens of E. A. PREBLE from Fort Resolution, June

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"Review of Canadian Botany" (Trans. Roy. Soc. Can. III. 4:4. 1897), where he expressly states that "with the exception of his immediate predecessors no botanist had accomplished more than PURSH to make the vegetation of Canada known." When JAMES published the manuscript of PURSH's traveling journal he did "not deal with that part of PURSH's work which was continued into and ended in Canada." "He made extensive collections chiefly through the province of Quebec, but all the material thus accumulated was subsequently destroyed by fire."

Regarding Lord SELKIRK, I have been informed by J. C. NELSON that "Lord Selkirk's Exp." probably refers to THOMAS DUNDAS, Fifth Earl of Selkirk, who (according to JOHNSON'S N. Univ. Cycl. 4:175. 1878) "spent several of the later years of his life in promoting emigration to the Red River of the North, British America." I have not yet been able to consult the tracts which he has published on emigration to those parts of Canada.

[14] Derived from πολιός, with white hair.

21, 1903 (nos. 196, 198; W.), which RYDBERG regards as "near *niphoclada* but with much broader and shorter leaves." The young leaves do not differ from those of the female specimen no. 194 previously cited, but the young male aments are very short, not exceeding 1 cm. in length and 0.5 cm. in thickness. Otherwise the flowers agree with those of var. *acutifolia*. If the size of the male aments should prove a reliable character, and if the male plant should belong to the same form as the female no. 194, this form might prove to be a new one more closely related to *S. cordifolia*. See also my remarks under *S. niphoclada* as to the size of male aments.

There is a male specimen collected by *Seton* and *Pringle*, July 19, 1907, near Caribou Island, Great Slave Lake (no. 43 [78305 O.]), which has been named *S. atra* Rydbg. by BALL. At first sight it resembles a great deal PREBLE'S nos. 196 and 198 mentioned above, but the leaves, which seem to be almost fully grown, measure only up to 3.6:1.6 cm. The flowers of the one small catkin (2.3:0.9 cm.) I could examine show no trace of a dorsal gland, and the hairy filaments are connected for $\frac{1}{3}$ to $\frac{1}{2}$ of their length. So far this form remains rather doubtful.

26. S. CORDIFOLIA Pursh.—The male syntype of *S. labradorica* mentioned (*l.c.* 345) bears the number 21, not 31, of WAGHORNE.

27. S. ANAMESA Schn.—In his Fl. Europ. 21:157. 1890, GANDOGER has described under *S. glauca* the following 4 new subspecies from Greenland: *S. eskimorum* (type: *Petersen*, Julianehaab); *S. groenlandica*, non Heer, nec Lundström (type: *Rink*, Godthaab); *S. platycarpa* (type: *J. Vahl*, Ikilok), and (*l.c.* 158) *S. Vahlii* (type: *J. Vahl*, Ikilok). Judging by the characters given in the key, all these names refer to a form having "folia anguste linearioblonga, 5–12 mm. lata," which are "supra semper canescentia et villosa vel tomentosa" in the last two forms, while they are "supra glabra aut glabrescentia et viridia" in the first two. Not having seen the types, I am unable to say to which species these forms really belong, but I presume they may be referable to what I have called *S. anamesa*. In giving binary names to those forms GANDOGER did the same as ANDERSSON did in several instances in his monograph. I believe, however, that these binomials cannot be regarded as

proper species, and therefore I do not think it advisable to take up one of GANDOGER'S names for *S. anamesa*.

V. SPECIES SECTIONIS INCERTAE. The proper systematic position of the following species is still doubtful to me, and most of them are so little known that it is impossible to even express an idea as to their affinities.

29. S. CHAMISSONIS And. in DC., Prodr. **16**[2]:290. 1868; Lundström apud Kjellman in Nordenskiöld, Vega Exp. Arbet. **2**:21 (Fanerogfl. St. Lawrence Ön). 1883; Coville in Proc. Wash. Acad. Sci. **3**:325. *fig. 23*. 1901.—*S. myrsinites* Chamisso in Linnaea **6**:540. 1831, non L.—The type of this rare but apparently well marked species was collected by CHAMISSO and ESCHSCHOLTZ in 1816 at St. Lawrence Bay; elsewhere it is only known from St. Lawrence Island and Port Clarence in Alaska.[15]

30. S. GLACIALIS And. in Öfv. K. Vet.-Akad. Förh. **15**:131. 1858; in DC., Prodr. **16**[2]:300. 1868; Coville in Proc. Wash. Acad. Sci. **3**:329. *fig. 24*. 1901; Rydberg in Bull. N.Y. Bot. Gard. **1**:262. 1899.—*S. Uva-ursi* Seemann, Bot. Voy. Herald 40. 1852, pro parte. —As COVILLE has already stated, "this species is known only from the type specimen collected by Lieutenant *W. J. G. Pullen* in 1849, on the Arctic seacoast between Point Barrow and the Mackenzie River, and from specimens collected at Point Barrow by *John Murdoch* in 1882–3." I have been able to examine a photograph and fragments of the type (*Pullen*, no. 155, f., fr. im.; K), and I agree with ANDERSSON that it is a forma *pusilla* of *S. ovalifolia*. The style is very short but not wanting, and the stigmas are relatively long; the pedicel is also distinct and in fruit about $\frac{1}{3}$ longer than the gland. It resembles the pubescent form of *S. ovalifolia*, which is only somewhat more vigorous, and shows a more distinct (but short) style. ANDERSSON describes the leaves of the type as

[15] After the manuscript of this note had gone to the printer, I found on a sheet with *S. amplifolia* of Herb. Cor. a male specimen of *S. Chamissonis* collected by B.E. on St. Lawrence Island, July 13, 1899, which had been seen by COVILLE but is not enumerated by him in 1901. Had I seen it before I finished my manuscript I would not have included this species in the present key because, judging by the male flowers, it seems to belong to sect. COMMUTATAE, with which I hope to deal later. The male flowers possess only one gland, and the fine and close acute serration of the leaves easily distinguishes this species from all the other willows treated in this paper.

"integerrima," while most of them in the specimen before me show a distinct but fine glandular denticulation in the lower half. Those of the type are entire, with the exception of a few minute teeth at the base of some leaves. They lack stomata in the upper epidermis. If I had seen the type before I finished the manuscript of this article, I would have placed *S. glacialis* next to *S. ovalifolia*, but as long as the male flowers are unknown the true affinity remains unknown.

31. S. VENUSTA And. in DC., Prodr. **16**^{2}:288. 1868, non Host 1828, from Sitka, of which, according to COVILLE, the description "suggests that the plant may prove to be a form of *Salix reticulata* grown in a shaded situation," can only be judged by an examination of the type material, which I have not yet had the opportunity to see.

32. S. OBCORDATA And. in DC., Prodr. **16**^{2}:291. 1868, which, like the preceding, came from Sitka, is even more obscure than that, and may prove to be another *S. reticulata* form or a hybrid of it with some other species. ANDERSSON himself placed it without number as *S. obcordata* between *S. ovalifolia* and *S. furcata*, but he says nothing about its relationship to these species, only mentioning its resemblance to *S. venusta* and *S. reticulata* in his more than meager description.

I hope that my notes may prove useful to other students of American willows, and I shall be most thankful to anyone who can correct any mistake I have made or furnish me with good material or information of these or other American willows. There are, of course, quite a number of specimens before me which I have not yet been able to elucidate. Among them are many which I suspect of being of hybrid origin, but I do not intend to deal with the hybrids until I have gained a more thorough understanding of all the American forms of this difficult genus.

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JAMAICA PLAIN, MASS.

MORPHOLOGY OF THE GENUS ACTINOMYCES. I[1]

CHARLES DRECHSLER

While the genus *Actinomyces* has received a large measure of attention in its relations to soil biology and to human, animal, and plant pathology, the natural affinities of the congeneric organisms that it has been customary to include in the group have been the subject of diverse opinions. Under a variety of synonyms, among which *Cladothrix*, *Nocardia*, *Discomyces*, and *Oospora* have been used nearly as frequently as *Actinomyces*, the group has been placed with the bacteria, with the Hyphomycetes, or assigned to an intermediate position. In the earlier publications on the ray fungus, including the papers by BOSTROEM (1)[2], and by WOLFF and ISRAEL (24), this organism was referred to the pleomorphic bacteria. The belief was seriously entertained that cocci, bacteria, and spirilla were produced by the plant, and in such regular succession that a number of investigators were led to draw up detailed ontogenetic schemes of considerable complexity. It is frequently not easy to determine the exact nature of the structures that were interpreted as pleomorphic stages. There are plenty of indications that contaminating bacteria were often present as secondary invaders; but more frequently aërial spores, segments of spiral or sinuous hyphae, and degenerative bodies of metachromatic substance were mistaken for schizomycetous types of nearly every description.

More recently *Actinomyces* has been frequently associated with the tubercle and diphtheria organisms on the assumption that they may represent a transition between the Hyphomycetes and the true Schizomycetes. A family of Actinomycetes has thus been erected as a natural group from these diverse components, united chiefly by resemblances in their staining reactions, a usual or an occasional filamentous habit, and the development of clavate elements in the animal body. It has been supposed by adherents of such a taxonomic disposition that either a progressive phylogeny

[1] Contribution from the Cryptogamic Laboratories of Harvard University, no. 83.

[2] The bibliography will appear at the end of Part II, which will be printed in February.

has occurred in the family, with *Actinomyces* at the head of a transition series developing increasingly well marked fungoid characteristics, or else that *Actinomyces* is the probable progenitor of the groups *Corynebacterium* and *Mycobacterium* by degenerative reduction.

The view that the ray fungus represents an organism with hyphomycetous affinities was advanced early by HARZ (7) and DEBARY (2). These authors regarded as conidia the clavate elements of the actinomycotic lesion, which BOSTROEM's studies later properly degraded to the rank of degenerative structures. SAUVAGEAU and RADAIS (20), DOMEC (3), THAXTER (22), GASPERINI (4), and others placed a number of congeneric forms among the Hyphomycetes on account of their production of aërial spores. It may be mentioned in this connection that an examination of a considerable number of species has convinced the writer that this disposition is the only one which is in harmony with the morphological conditions represented in the genus.

The material used in these studies, with the exception of authentic cultures of the species described by WAKSMAN and CURTIS (23), and of a number of organisms isolated by H. J. CONN from soil collected near Geneva, New York, was largely obtained from soil collected in Cambridge, Massachusetts. By the use of the dilution method more than 1000 plants belonging to the genus were isolated from this source; and of these about 300, representing probably more than 100 species, were selected for morphological examination. Approximately 400 additional individuals were derived from soil collected in Porto Rico, Cuba, Panama, Montana, Wisconsin, and Kansas, as well as from outdoor air, tap water, horse manure, and gross cultures of dung, dead leaves, and other vegetable matter. The potato scab organism was obtained from Mr. M. SHAPAVALOV, who had isolated it from a diseased tuber, and experimentally established its pathogenicity.

The morphology of the vegetative thallus of *Actinomyces*, apart from its astonishing minuteness, the diameter of the filaments ranging commonly from 0.5 to 1.2 μ, presents no features unusual among the fungi. In most species the mycelium is generally sparsely and irregularly septate; and although in other forms trans-

verse walls may appear with somewhat greater frequency, there are none in which septation approaches any pronounced degree of regularity or closeness. Ramifications are abundant, and the branching is altogether of the "true" type. MACÉ (15), who first carefully observed the formation of branches, found it to proceed by the elongation of lateral buds arising some distance back from the growing point of an axial filament, the branch thus produced giving rise similarly to secondary branches by lateral proliferation. LACHNER-SANDOVAL (12) confirmed MACÉ, designating the process as monopodial and denying the existence of true dichotomy in the genus, which had been affirmed by previous investigators. Later NEUKIRCH (18) reported that the branching in *Actinomyces ochroleuceus* was occasionally of the nature of a true dichotomy. From an examination of very young mycelium (fig. 3)[3] it is apparent that, at least in stages following the germination of the spore, filaments are not infrequently terminated by two elements too closely similar in size and angular relationships to be distinguished as bud and axial tip. The branching in such cases must be regarded as dichotomous, although all gradations toward the prevailing well defined monopody may be found. It seems reasonable to suppose, however, that the distinction is one of convenience, not implying any fundamental difference in manner of development.

The cytological structure of *Actinomyces* is equally devoid of bacterial characteristics. The branches forming the periphery of the actively growing pellicle, or the young sporogenous branches attached at intervals to the superficial mycelium, are filled with dense protoplasm, which, with haematoxylin, takes a deep homogeneous stain. Further toward the origin of the hyphae the contents become more attenuated, and vacuoles appear, increasing in number and size until they occupy the larger portion of the filaments. When individual vacuoles become excessively large and extend through a considerable length of filament, the cytoplasm is in a large measure confined to a peripheral layer, a condition which led NEUKIRCH to distinguish a thin, strongly refringent "Aussenplasma" and a less refringent "Innenplasma."

[3] The plates will appear in connection with the second part, to be published in the following number.

The presence of large vacuoles is commonly associated with local distentions of the filament wall. These may occur with such regularity in the degenerate mycelium of some species as to suggest the appearance of *Leptomitus*, each swollen segment being largely occupied by a single elliptical vacuole, separated from the vacuole in the adjacent distention by a protoplasmic partition at the constriction (figs. 47, 48, 106). In other species and quite generally in the nutritive mycelium of all forms, that is, the mycelium immersed in the substratum, no marked regularity in the alternation of inflated portions and constrictions is observable; but pronounced deviations in the diameter of filaments may occur with more or less variable frequency.

A great deal of importance has been attributed by some writers to a variety of abnormalities and products of degenerative changes occurring in the thallus of *Actinomyces*. In the earlier literature on the ray fungus, especially in the publications of ISRAEL (**8**), JOHNE (**9**), and MACFADYEAN (**16**), bodies described as "micrococci," "cocci," or "coccus-like granules" were given minute attention, and assigned an important rôle in the complex ontogeny ascribed to the parasite, then supposed to belong to the pleomorphic bacteria. WOLFF and ISRAEL (**24**), whose photomicrographs of these bodies leave no reasonable doubt about their identity with structures very frequently observed by the writer (figs. 15, 31, 32, 42, 91), confused them with the spores reported by other authors; and as the structures did not possess the heat resistance common to spores of bacteria, these investigators were inclined to question the production of spores by *Actinomyces*. Since the organism used by WOLFF and ISRAEL was constantly sterile, their conclusion concerning it was undoubtedly correct. BOSTROEM, who experimented with a sporiferous form, did not succeed in avoiding the same confusion, and refers indiscriminately to the unicellular products formed from aërial hyphae, and to the spherical endogenous granules, as "spores."

Round granules, deeply stained in the living filament by very dilute methylene blue, were studied later by NEUKIRCH. He noted in them a variable size, a method of multiplication, and an orientation related to the regions of growth in the thallus. These

observations led him to believe that the structures represented nuclei. SCHÜTZE (21), who applied NEUKIRCH'S method of staining, designated the bodies as metachromatic granules. After an examination of their occurrence in the aërial mycelium of a considerable number of species, such an interpretation seems, in the opinion of the writer, to offer the greater degree of plausibility.

The metachromatic material is easily distinguished by a powerful affinity for most of the stains ordinarily employed in laboratories. In material fixed in alcohol, and treated with Delafield's hematoxylin, it retains a nearly opaque stain after all other structures have been completely decolorized. Indications of its presence in the tips of growing filaments, or in sporogenous branches, in general are very infrequent. Some distance toward the origin of the hyphae, associated with a more attenuated or vacuolated protoplasm, the material makes its appearance in the form of rather minute granules widely separated from one another. As the filament is followed still farther back, the granules increase in size and frequency; often their arrangement is one of much regularity, the individual spherical bodies being of nearly equal size, exactly filling the lumen of the filament, and separated by nearly equal spaces (fig. 42). In other cases the granules seem to coalesce and occupy entire segments of hyphae (fig. 32); and in a few species extensive portions of mycelium were frequently found entirely filled with long unbroken masses of metachromatic substance. It is this property of coalescence of smaller granules, to form incomparably larger masses, bearing out the similarity in appearance to a homogeneous liquid with a relatively high surface tension, that makes it difficult to believe that we are dealing here with anything relating to spores or to nuclei.

The function of the metachromatic material in the *Actinomyces* thallus cannot be ascertained with certainty. A number of views have been advanced regarding the rôle of metachromatic substance in the cell, none of which has gained universal acceptance. The best explanation, in the opinion of the writer, seems to be that it represents an occluded waste product. While its presence in small or moderate quantities in the sterile hyphae bearing the sporogenous branchlets is probably more or less normal, its abundant

occurrence here, as everywhere else, is an indication of advanced degeneration. In the more mature mycelium of *Actinomyces* VIII (fig. 47) metachromatic granules are usually very conspicuous, often occupying most of the space in the narrowed constrictions between the large vacuoles in the highly inflated mycelial segments. The appearance of such a thallus is not in the least suggestive of the structure of bacteria, and indicates that the resemblance between *Actinomyces* and the true Schizomycetes in the consistency of protoplasm, emphasized by some writers as an important phylogenetic connection, has been unduly overestimated.

While the sterile filaments in the nutrient and in the aërial mycelium are relatively uniform in structure throughout the genus, the sporogenous apparatus of many species exhibits a large degree of morphological individuality. This diversity has not usually been recognized by writers, and has undoubtedly been responsible for a portion of the controversy that has arisen, particularly with regard to the method of spore formation. LACHNER-SANDOVAL (**12**), from a study of *Actinomyces albido-flava*, distinguished two kinds of propagative bodies: (1) fragmentation spores appearing as spherical to cylindrical segments in old hyphae, formed by a contraction of the protoplasm; and (2) segmentation spores developed by a septation of the tips of aërial filaments. Segmentation was usually found to involve only lateral branches coming from aërial hyphae, but in submerged growths it frequently extended also to the main filament, leading to the development of a dendroidic system of spore chains. LACHNER-SANDOVAL'S figures of these formations, however, are much less striking than might be expected from the description in the text, and do not convey the impression of ramifications approaching treelike proportions.

NEUKIRCH identified the segmentation of LACHNER-SANDOVAL with oidium-spore formation among the fungi, and abandoned the use of a specific term. He vigorously disputed the development of aërial spores by a septation of the mycelium. According to his account the spores are formed as the result of successive contractions of protoplasm until approximately isodiametric portions are separated by regularly alternating empty spaces. This process he identified with the fragmentation of MACÉ, localizing it in a differ-

ent region from LACHNER-SANDOVAL, and properly relegating the fragmentation of the latter to the category of degenerative changes.

GILBERT (5) found some lateral branches to begin the process of forming spores by becoming differentiated into highly refractive and weakly refractive portions. Constrictions later appear, unassociated with visible changes inside the filament, and soon the spores are completely cut off. GILBERT designated the process as segmentation, following LACHNER-SANDOVAL, who, however, had actually observed septa appearing more or less simultaneously with the constrictions, their appearance being followed by the enlargement and rounding up of the segments to form spores.

MIEHE (17), in his study of *Actinomyces thermophilus*, only incidentally examined the mode of sporulation. He believed spores were produced singly on very short stalks attached laterally to the main hyphae, or possibly by successive contractions in chains. In either case conidia were produced, not by the segmentation of a completed filament, but by the development of a structure which at no time constituted a cylindrical, continuous hypha. This account, in general, bears strong resemblances to the later description by SCHÜTZE (21) of *Actinomyces monosporus*, a form in which the spores are borne singly on delicate stalks in racemose arrangement on a thicker axial filament. It might well be questioned, however, whether forms like this, which depart so widely from the main morphological trend of *Actinomyces*, are properly to be assigned to this genus, even if allowance is made for much liberality in the definition of hyphomycetous form-genera.

The same criticism, however, cannot be extended to the condition described by SCHÜTZE in his strain of *Actinomyces thermophilus*. In his account of this species its author strongly defended NEUKIRCH's position that the mode of sporulation was one of fragmentation. However, while NEUKIRCH found long filaments converted into spore chains by successions of protoplasmic contractions, the long portions finally becoming resolved into ultimate spores, SCHÜTZE found that only short terminal portions or short lateral branches yielding about 5 spores were involved. According to NEUKIRCH, the slightly refractive spaces between the masses of protoplasm that later develop into spores are entirely empty, and

the intervening portions of filament wall merely collapse as the spores mature. SCHÜTZE believed that these intervals were filled with attenuated protoplasm, and that by their constriction the spores were delimited without the evacuation of portions of hyphal wall. The spore of NEUKIRCH, consequently, is a structure possessing its own spore wall, enveloped, except at its ends, by the remnants of the old filament wall; that of SCHÜTZE, on the other hand, is without a separate spore wall, the filament wall constituting the only membrane present, and forming a spherical shell everywhere inclosing the protoplasm.

NEUKIRCH gave much attention to certain structures he designated as oidium-spores. They developed in submerged growths, the transformation of the filament consisting only in more or less close septation, followed by a slight swelling of the segments. Under suitable conditions filaments grew out from them, an occurrence NEUKIRCH regarded as germination. "Aussenplasma" and "Innenplasma," in his opinion, were sharply defined, but a spore wall was absent. The elements did not exceed the filaments in resistance either to heat or desiccation. NEUKIRCH believed their function to be the dissemination of the fungus in liquid media.

LACHNER-SANDOVAL seems to have seen the same structures and regarded them as segmentation spores that had developed in the submerged condition. GILBERT, SCHÜTZE, and KRAINSKY (10) record their failure to find these bodies without, however, denying their existence. According to SCHÜTZE and GASPERINI, sporulation may occur in hyphae which are not truly air hyphae.

It seems questionable whether any desirable end is served by calling NEUKIRCH's elements spores at all. To apply the term to structures with so little individuality, even though a sort of promiscuous viability may be attributed to them, is approaching very close to the point where all bodies not filaments of uniform thickness are to be regarded as spores. Certainly the distended elements in old mycelium of *Actinomyces* VIII (figs. 47, 48), which represent enlargements of axial filaments developed gradually in the course of time at the junctures with moderately complex systems of sporogenous hyphae, frequently have an equal or greater resemblance to reproductive bodies; and the behavior, under similar

conditions, of forms like the smuts, *Mucor*, and *Penicillium*, would make advisable a larger measure of caution in dealing with fungi growing irregularly in a submerged condition.

Although various details associated with the sporulation of *Actinomyces* have thus been dealt with in the literature, the opinion still seems to prevail widely that the process is of an irregular and miscellaneous nature. LITMAN and CUNNINGHAM (14) in recent years have denied the character of spores to the "gonidia" produced by the potato-scab organism; the elements are believed simply to "serve as a segment of the mycelium, which, by increasing the number of segments, may increase the chances for spread and continuous existence." This view seems, in the opinion of the writer, very much at variance with the distinctiveness of the well characterized sporogenous apparatus found in *Actinomyces*.

In pursuing the present studies a method of mounting material was employed which, in view of the exceptional fragility of all species of *Actinomyces*, and the great difficulty ordinarily encountered in attempting to stain undisturbed sporulating conditions, gave exceptionally good results. The plants were grown on a suitable substratum, usually potato or glucose agar. Growth on potato agar, as a general rule, is more prompt and productive of mycelium; but as its use, especially with species exerting a strong tyrosinase reaction, stimulates to excessive guttation and disruption of the sporophores by the extruded droplets, a medium not possessing this property is often found to be advantageous. After the cultures had attained a proper degree of maturity, the whole growth was cut from the agar and removed from the tube as carefully as possible. A slide smeared with albumen fixative was now brought into firm contact with the mycelium and then separated from it, precautions being taken to avoid altogether any sliding of the two surfaces on each other. If the growth is not too young, this procedure will leave the upper portions of the aërial mycelium adhering to the slide without serious disarrangement, and killing and fixation may be at once effected by the use, for example, of strong alcohol. The material was subsequently stained and mounted in balsam. The quality of preparations in which the spore chains have commenced to disintegrate in large numbers is

impaired by the presence of large masses of free spores, which retain their staining properties for some time after maturing. Later the spore walls seem to become entirely impervious to stains, and as a result when the secondary mycelium develops beyond a slight clouding effect no difficulty is encountered from this source. The best results are obtained when the print is made soon after the mycelium begins to adhere readily to the smeared slide.

The nature of the killing agent employed was found to have no noticeable effect on the preparation. Flemming's mixtures, both weaker and stronger, picro-formol, picro-acetic, Carnoy's fluid, and 95 per cent alcohol were tried with apparently the same results. Owing to the small diameter of the filaments, the penetration is probably so nearly instantaneous that plasmolysis is effectively prevented by nearly any toxic agent capable of readily wetting the material. In order to obviate the necessity of washing, strong alcohol was used almost exclusively.

Much more depends on the proper choice of a stain. Saffranin, gentian violet, Bismarck brown, and eosin usually fail to bring about a sufficiently deep coloration. Carbol-fuchsin acts powerfully and rapidly, but is poor for purposes of differentiation. Haidenhain's iron-alum haematoxylin is good for protoplasmic structures. The most satisfactory results were obtained with Delafield's haematoxylin, which if allowed to act for 24 hours, with the proper degree of decolorization, yields deeply stained, clear preparations, showing vacuoles, metachromatic, and nuclear structures, as well as septa, with remarkable distinctness.

The spores of all species of *Actinomyces* are developed by a transformation of more or less specialized hyphal branches distinguishable from the sterile hyphae of the aërial mycelium at an early stage in their development. In general, with the exception of such inflated hyphae as are shown in figs. 47, 48, and 106, the diameter of any portion of sterile mycelium is attained at the time it arises through the elongation of the growing filament tip, subsequent increase in thickness being very slight. The sporogenous branches, however, are in the beginning conspicuously thinner than the axial hyphae from which they are derived. Later, when their final linear extension has been nearly attained, increase in thickness

generally follows. This increase may be slight, as in some species in which the mature sporogenous hyphae are still somewhat thinner than the vegetative hyphae (fig. 46), or more considerable, as in forms in which they conspicuously exceed the latter in thickness (figs. 4–6). The very simple type represented by *Actinomyces* XIII, in which the aërial mycelium is represented by very long filaments, rarely branching and apparently sporogenous almost to their point of origin in the nutritive mycelium, constitutes the only exception, since in this instance there is no indication of thickening in the young fertile hyphae, nor indeed any variation in the diameter of its vegetative filaments.

In a majority of the species the maturation of the sporogenous hyphae is associated with a peculiarity in growth by which they become coiled in more or less characteristic spirals. The tendency toward the coiled condition is usually clearly manifested before the branch has grown to half its final length through the open flexuous habit of the young filament (figs. 5*c2*, 107). As elongation continues, the turns become increasingly definite, but the contraction leading to the final condition, which ranges from that illustrated by *Actinomyces* XIII with its open, barely perceptible turns, to one in which the spirals are so strongly compressed that its adjacent turns are in continuous contact (figs. 44, 51, 57) in a fashion resembling that of the spores of the hyphomycetous genus *Helicoön*, is usually delayed until the later growth in thickness of the filament. Specific differences may not only be indicated by the obliquity of the spiral, but involve also the number and diameter of its turns, and its construction with reference to the dextrorse or sinistrorse condition. The range in different species extends from the 2 or 3 turns exhibited in forms like *Actinomyces* II and XVI, to over 20 turns in others; but the range in a particular species is always considerably smaller. The writer once observed a spiral with 24 turns, but this probably approximates the extreme maximum; spirals with 14–16 turns (figs. 23, 57, 94*c*) are by no means abundant, and probably no species produces many in which there are more than 12 turns.

The diameter of the spirals as a whole is more or less in inverse ratio to the number of turns characteristic of the species. This

correlation is very evident in a comparison of types like *Actinomyces* II and XVI showing spiral sporogenous hyphae with a few wide turns, and types like IV, V, and XVII illustrating spirals of many narrow turns.

Rotation in the formation of spirals is specifically sinistrorse or dextrorse in different species of the genus; and it is interesting to note that here, as in the vegetable world in general, sinistrorse are much more abundant than dextrorse species. Of the 17 species with spiral sporogenous branches figured in the present paper, which have been selected as representative of a much larger number, 5 are dextrorse, 11 are sinistrorse, while the condition of the remaining one could not be ascertained with certainty. In general, the proportion appears throughout the entire genus. As a morphological feature, the absolute constancy with which a species adheres to one kind of rotation is noteworthy, particularly in view of the extremely minute dimensions of the structures concerned.

An examination and comparison of the relation of the sporogenous branches to each other, and to the axial filaments, enables one to recognize several tendencies, the distinguishing characteristics of which are correlated with differences in the sequence of proliferation. Two main types may thus be recognized, approaching each other in apparently intermediate forms, but moderately distinct at the extremes: (1) an erect dendroidic type in which the sequence of development of the sporogenous hyphae is successive; and (2) a prostrate, racemose type in which the development is more nearly simultaneous.

In the erect type, well exemplified in *Actinomyces* I, the development of the fructification starts from a single erect hypha with a spiral termination. Sporogenesis commences at the tip by the insertion of regularly spaced septa, and proceeds downward toward the base of the filament. Usually before much of the hypha has been involved, a single septum will appear well toward its base, and immediately below it the bud anlage of a new sporogenous branch appears. As the latter is attaining its growth in length and thickness, and its spiral disposition, the basipetal septation in the axial filament proceeds to the septum above the insertion of this first branch, the young spores thus delimited undergo maturation

processes, the spiral becomes relaxed, and the chain of spores subject to disruption. The branch now passes through the same course of development as the axial filament and in turn gives rise to a sporogenous branch below a septum a little above its own insertion. The number of sporogenous branches developed below a single septum is generally increased to several by proliferations subsequent to the first; and as the initiation and development of successive orders may be indefinitely repeated, complex fructifications are frequently developed, in which a succession of the processes described are simultaneously taking place at many points.

In the second type there is no such clearly defined relation between younger and more mature sporogenous hyphae. Development of a fructification is initiated by the proliferation of branches at irregular intervals on the distal portion of a prostrate axial filament which often exceeds 1 mm. in length. The branches may either stop their more extensive development after forming a spiral, or themselves proliferate a secondary branch a short distance above their own insertion; and this in turn may form a spiral and give rise to a tertiary branch (fig. 43). By a repetition of this process each lateral element may become branched several times, the whole apparatus as well as its insertion on the axial filament being characterized by an absence of septa. Sporulation, instead of beginning in any individual spiral as soon as it is formed, is usually delayed until the branching and growth of spiral hyphae in the same lateral process have come to an end (figs. 42–44, 46), when it will often proceed rapidly and almost simultaneously in all the spirals (fig. 41). The termination of the axial filament itself develops into a spiral, and behaves essentially like a primary lateral branch.

Occasionally the axis of one of these racemose arrangements may be comparatively short, resulting in a rather intricate structure in which the spirals of one lateral branch may be entangled with those of another (fig. 44). The tendencies characteristic of the type, however, are maintained: the absence of a septum above the insertion of branches, and the delay in sporulation in the spirals first formed, until the growth of the last order of sporogenous branches is more or less complete.

In addition, however, to species in which these two types are clearly distinguished, a still larger number of species present a combination of the two features. Frequently the open racemose arrangement of the lateral branches on the main axial filament is associated with a successive order of development in the further ramifications of the branches (figs. 63, 79). The presence of a septum above the insertion of a branch is characteristic of more species than is its absence (figs. 2, 5*c*); and in some species both conditions prevail (figs. 53, 79, 81). In other forms a fructification with successive development may terminate a long prostrate filament.

In a few species, particularly *Actinomyces* X and XVIII, there are formed, in addition to the more regular fructifications, others of a more miscellaneous tendency. The branching axial filaments are relatively thick, densely filled with protoplasm, and bear at very close and irregular intervals a short, thick, unbranched sporogenous hypha with little or no spiral modification (fig. 103). It seems quite probable that this type of development is associated with the excessively rapid growth that characterizes the two forms in which it was most frequently observed.

The degree of completeness to which the aërial mycelium of *Actinomyces* is converted into spores has generally been overestimated. On the contrary, sporulation is quite strictly confined to terminal elements, never as a rule passing beyond the first junction with another element. The proliferation of the branch nearest the end of the axial filament limits spore production in this filament to the portion beyond the insertion of the branch; and in the same manner the proliferation of a secondary from a primary lateral branch results in a sterilization of the portion of hypha below the insertion of the new branch. In one species, *Actinomyces* V, sporulation is even further restricted by the apparent abortion of a number of potential spores at the proximal end of the unbranched lateral branches. The hyphal portion involved first develops as usual, but when the characteristic septation associated with the delimitation of spores in this species appears in the spiral, it is not extended to the base of the branch, although indications of regularly spaced membranes may usually be distinguished (figs. 21,

24, 25). Later the unsegmented portion is gradually evacuated and converted into a sterile stalk devoid of protoplasm (figs. 29, 30). It is interesting to note that the basal septum, which in an allied and very similar form, *Actinomyces* VI, delimits the lowest spore from the axial filament, here also is present as a well developed cross-wall.

The delimitation of the ultimate cells in the process of sporulation occurs usually as the growth in thickness and the contraction of the spiral (where this is present) are approaching a stage of completion. It has usually been believed by investigators that the details connected with spore formation are uniform throughout the genus. This belief, which the writer was at first inclined to share, must be considerably modified in view of the diversity of conditions actually found. In most species the sporogenous hyphae become divided into regular cylindrical cells separated by septa; the latter generally stain deeply with Delafield's haematoxylin, probably as the result of an association with metachromatic or possibly nuclear material. The species which are thus characterized by clearly defined septation may be assigned to three different categories, separated by differences in the disposition of their septa and in the development of their spores.

In the first category, represented by *Actinomyces* I, the cross-walls in the sporogenous hyphae remain without any very pronounced change, continuing to separate the adjacent cells until these have developed into a chain of mature contiguous spores. The insertion of these septa progresses from the tip toward the base, and does not break the physiological continuity of the hyphae; for food material apparently is readily transported through them to the young spores at the termination, since these subsequently increase in size, and may deposit a wall of measurable thickness.

In the second category the septa apparently split into halves, which are then drawn apart by the longitudinal contraction of the individual protoplasts (figs. 5*c1*, 8*a–f*, 59). In *Actinomyces* II the very pronounced growth in thickness of the sporogenous hyphae, following the insertion of septa, indicates that in this species also septation brings about no impediment in the transfer of food material. This is particularly remarkable on account of the

extraordinary thickness of the septa characterizing this species. *Actinomyces* XVII, however, while less striking, probably represents more nearly the usual condition prevailing in the second category. The segment of the filament wall evacuated by the contraction of each two successive spores undergoes no change until fractured by the disruption of the chain of mature spores.

In the third category (*Actinomyces* IV, V, VI, VII, and XII) the cross-walls first undergo a deep constriction, which by involving the ends of the young cylindrical spores gives to the latter an elongated ellipsoidal shape (fig. 70*a–d*). The constricted septum now gradually loses its staining properties, and appears to become slightly drawn out in a longitudinal direction (fig. 70*e*). A preparation stained with Delafield's haematoxylin usually shows many old spore chains in which the individual spores are thus connected by hyaline isthmuses. Occasionally an isthmus may be found with a remnant of the old deep staining septum still unchanged in its center (figs. 16, 70*e*).

Beyond these three types of sporulation another must at least be provisionally recognized, in which septa are either absent from the developing sporogenous hyphae, or are not demonstrated by the use of ordinary stains. The protoplast appears to contract at regular intervals, yielding a series of non-contiguous spores, held together for a time by the connecting segments of evacuated filament wall (fig. 73). It is this type of sporulation which NEUKIRCH and his followers, in opposition to LACHNER-SANDOVAL, believed to prevail throughout the genus. NEUKIRCH'S conclusion that septa are never involved in the sporogenesis of *Actinomyces* certainly cannot be extended to the large majority of species; and its application to any forms whatsoever is associated with some reasonable doubt. The writer is inclined to believe that cross-walls appear in the development of the sporogenous hyphae probably throughout the genus, but in some members are too thin to be recognized as distinct septa. Such an interpretation is suggested by the wide range in the thickness of septa found to occur, from the very massive structures of *Actinomyces* II, through those of moderate thickness in *Actinomyces* I, XII, and XVI, to the condition prevailing in

Actinomyces III and VIII, where cross-walls can only rarely be distinctly perceived.

All investigators, with the exception of SCHÜTZE, agree in attributing to the peripheral wall of the filament of *Actinomyces* an extreme thinness. Indeed, KRUSE (11) and others have urged the single contoured character of the membrane as an evidence of the bacterial affinity of the genus. It is only necessary to examine fungus forms like *Chlorosplenium* or *Phoma*, to convince one's self that the single contoured wall is generally characteristic of minute cells, whatever their taxonomic connections may be. Yet while the phylogenetic inference may safely be rejected, it still remains true that the peripheral wall of every species of *Actinomyces*, except possibly those of some old enlarged hyphae, cannot be made out as a distinct structure with double contour. In evacuated portions its location is indicated by only the faintest indication of its outline. Nor is this surprising when we consider that the maximum resolving power of any combination of lenses employing visible light is approximately 0.17 μ. As this magnitude barely equals the widths of the thinnest cross-walls observed, it is not difficult to suppose that, in the type of sporogenous hyphae represented in *Actinomyces* XIII, the dimensions of the partitions, like the filament wall generally, fall below the limit of visibility.

It is pertinent in this connection to emphasize the peculiarity in the nature of the cross-walls, the appearance of which in many species of *Actinomyces* initiates the development of the individual spores. Their unusual relative thickness, even in species in which they can be distinguished only with difficulty, but where nevertheless their thickness must exceed 0.17 μ, in filaments with a diameter of only 0.9 μ, is indicative of a composition essentially different from that of the peripheral wall. This indication is strengthened by the strong affinity for dyes characteristic of the septa, the evident ease with which they permit of the passage of food material, and their apparent plasticity of behavior, resulting in a median split in some species, and in others in a gradual constriction followed by a slow transformation into an attenuated isthmus.

The disappearance of the deep staining derivatives of the septa from the ends of the young spores is in some species accompanied

by the appearance of one or several deep staining granules within the spore. Whether the latter represent nuclei or bodies of metachromatic material cannot definitely be determined. It seems not at all improbable, however, that some of the structures that can be differentiated within the more mature spores, particularly those characterized by uniform size and moderate staining properties (figs. 1, 2, 33, 35) are nuclei. In *Actinomyces* IV and XII they may frequently be distinguished comparatively early, before the septa, with which they alternate in regular succession, show any perceptible constriction, indicating that their existence is not related to the subsequent disposition of the partitions (fig. 67). When two of these bodies occur in the same spore they uniformly occupy opposite or diagonal positions (fig. 2, *a*, *d*2). The question arises why these bodies, if they actually represent nuclei and not structures originating *de novo*, cannot be distinguished in the young continuous sporogenous hyphae. The only explanation that can be advanced is that the protoplasm in the earlier stages is too dense to make possible any conspicuous contact between cytoplasm and nucleus. Later, with the attenuation and vacuolization of the cytoplasm that occur with the maturation of the spore, apparently as the result of the deposition of a special wall, the nucleus becomes increasingly distinct, and in some species it constitutes the only spore structure clearly visible in the stained preparation (fig. 41).

It cannot be denied, however, that granules having more the appearance of the metachromatic granules found in degenerate sterile filaments occur in the spores of some species, either alone or together with a nucleus-like body. They differ from the latter in taking a deeper stain; in having an absolutely smooth contour; in offering considerable variability in size; and when present in numbers assuming no definite orientation with reference to each other. They have been noted in those species in which the septa associated with the delimitation of spores is particularly massive; and in *Actinomyces* II (fig. 8*f*) their derivation from the excessive wall material seems reasonably well established. After the septa have separated along a median plane, the deep staining substance at each end may contract, yielding a number of spherical bodies inside of the spore. This process is probably of a more or less

pathological nature, since in the usual type of development the wall material is gradually distributed through the inclosed protoplasm, causing the normal mature spore, except for the presence of a vacuole, to take an almost homogeneous stain.

Another indication of the similarity in nature existing between metachromatic material and the deep staining transverse septa of *Actinomyces* is found in the occurrence of both within peculiar large spherical structures. These structures appear generally to occupy nearly the entire lumen of the filament, and not infrequently are related to local enlargements. Occasionally, however, their diameter is considerably smaller than that of the hyphae (fig. 103). In any case they may contain either one or several peripherally located metachromatic granules, or a uniformly thick, well defined, deep staining, transverse septum, exactly median in position. It is interesting to note that whenever granules occur their surfaces in contact with the periphery of the structure represent portions of convex spherical surfaces conforming accurately to the confining surface; and whenever a septum is found traversing one of these structures considerably smaller in diameter than the filament, it does not extend into the protoplasm, but remains in its finished state as a curious partial partition.

The germination of the spores of *Actinomyces* takes place readily in dilute nutrient solutions, such as 1 per cent glucose solution, or nearly any vegetable decoction. During the first few hours of incubation at a moderate temperature they increase considerably in volume by swelling. From 1 to 4 germ tubes are then produced, apparently more or less successfully, the approximate number being, in a measure, characteristic of the species. Specific characteristics are expressed also in the diameter of the hyphae, and in the frequency of branching.

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PROTOMARATTIA, A NEW GENUS OF MARATTIACEAE, AND ARCHANGIOPTERIS

(WITH PLATE I AND THREE FIGURES)

BUNZO HAYATA

The Marattiaceae constitute a small family which may be regarded as the survivor of a much larger group. At present only 6 genera are known: *Archangiopteris*,[1] *Macroglossum*,[2] *Angiopteris*, *Marattia*, *Christensenia* (*Kaulfussia*), and *Danaea*. *Archangiopteris* was first discovered by A. HENRY in Yunnan and was published in 1899 by CHRIST and GIESENHAGEN as a genus connecting *Angiopteris* with *Danaea*. The type of the genus *A. Henryi* is shown to be one of the most primitive forms of Marattiaceae by its simply pinnate leaves and simple stelar structure.[3] According to GWYNNE-VAUGHAN,[4] the mature stem of *Archangiopteris* retains a stage which is rapidly passed through by the young plants of *Angiopteris* and other genera. The same seems to hold true as to the form of the leaves. As far as I have observed *Angiopteris* in its habitat in Formosa, the first 2 or 3 leaves from a young stock usually are simply pinnate, but die before they reach maturity and become fertile. The pinnae of these first leaves are much larger than of those that follow, and closely resemble those of *Archangiopteris* in shape and size. We may infer, therefore, that *Archangiopteris* represents the form of a primitive type to which the ancestor of *Angiopteris* may have belonged.

Archangiopteris is most closely related to *Macroglossum*,[5] recently established by COPELAND, both in the simply pinnate fronds and

[1] CHRIST, H., and GIESENHAGEN, K., Pteridographische Notizen. Flora **86**:72–85. 1899.

[2] COPELAND, E. B., The ferns of the Malay-Asiatic region. Philipp. Jour. Sci. **4**:1–64. 1909.

[3] LOTSY, J. P., Vorträge über botanische Stammesgeschichte **2**:676. 1906.

[4] GWYNNE-VAUGHAN, D. T., On the anatomy of *Archangiopteris Henryi* and other Marattiaceae. Ann. Botany **19**:268. 1905.

[5] CAMPBELL, D. H., The genus *Macroglossum* Copeland. Philipp. Jour. Sci. **9**:199–223. 1914; The structure and affinities of *Macroglossum Alidae* Copeland. Ann. Botany **28**:651–669. 1914.

in the elongated linear sori, but differs from it in the absence of ridges between the sori and in the dorsiventral rhizomes. GWYNNE-VAUGHAN (*loc. cit.*) says that in the specimens examined by him there was no suggestion of dorsiventrality in the rhizome of *Archangiopteris*, and the leaf arrangement and the vascular structure indicated a radial symmetry. So far as I can judge from the figure given by the author,[6] however, there are some indications of dorsiventrality in the rhizome, as can be seen in the upward bending of the stipes of the leaves and in the fact that the rhizome ascends somewhat obliquely toward the apex; and it also may be inferred that the remaining portions of the rhizome not given in the figure very probably run horizontally. In *Archangiopteris Somai*, recently discovered in Formosa, and two other new species from Tonkin, which will be described later, the rhizomes are prostrate and show very clear signs of dorsiventrality.

In the summer of 1916 I was sent to Tonkin for collecting. I found there two new species of *Archangiopteris* and a type of a new genus closely related to the latter. All these plants present an appearance very similar to other ferns, such as *Coniogramme japonica*, *C. fraxinea*, *Diplaziopsis javanica*, or *Diplazium bantamense*, and occur in very small numbers amidst a multitude of the previously mentioned ferns. As it is very rarely that one has the opportunity to meet with these plants of *Archangiopteris* and the allied new genus, it may not be entirely out of place if I should tell how I was led to discover these very rare and interesting ferns.

Some 10 years ago I was greatly interested in learning of HENRY'S discovery of *Archangiopteris*, representing as it did an ancient type of the Marattiaceae, and I wondered whether there might not exist another species of the genus in Formosa, the flora of which I have since then been studying. In 1915, when examining collections sent by the late T. SOMA from Formosa, I found among them a curious looking fern labeled *Gymnogramme japonica*. A glance at the specimen showed me that it was another type of *Archangiopteris*, which was then named and published as *A. Somai*.[7]

[6] GWYNNE-VAUGHAN, D. T., *loc. cit. pl. 10. figs. 1* and *2*.

[7] HAYATA, B., Icones Plantarum Formosanarum. **5**:256; **6**:154. *pl. 19*.

The next year I went to Formosa to the native place of the plant on the bank of a rivulet in a dense forest at an altitude of about 2000 ft. in the northern part of the island, for I wished to see a living specimen of this highly interesting fern. On the first day of our search we were not successful. The difficulty of finding it is partly due to its extreme rarity and partly to its existence only among other ferns closely resembling it in external appearance. On the second day I was at last successful in finding a few specimens of *Archangiopteris Somai*.

In the summer of 1917 I went to Chapa in the mountainous regions on the boundary between Yunnan and Tonkin. There too I wondered if I might not have the opportunity of finding some *Archangiopteris*, and so I made a careful search, turning back the leaves of all similar ferns which I came across. At last, as I had expected, I found a stock of the desired genus, in the shade of the forest at an altitude of about 4000 ft., between Chapa and Mueng-Xen. It was just a single stock. The fern resembled *A. Henryi*, but differed from it in the absence of indusium scales in the middle of the sori. It was a new species which I propose to call *A. subintegra*, a description of it being given in the present paper. Later on I went to Mt. Tamdao in the central part of Tonkin, and collected in a forest at an altitude of about 3000 ft. There I saw on the side of the forestry service path one poor specimen which I thought most certainly a species of *Archangiopteris* before examining the fern. It was a sterile specimen, yet I believed it to be a plant of the same genus, until I found near by some fertile specimens. They revealed the fact that they were different from *Archangiopteris* in fructification, all other characters being exactly like the latter. The sporangia of the newly discovered plant were quite fused together, reminding one exactly of those of *Marattia*, but differing from the latter in the long linear synangium. I thought that it might be a type of a new genus intermediate between *Archangiopteris* and *Marattia;* but I shall refer to this later. Not very far from there I collected a true *Archangiopteris*, another new species, which I propose to call *A. tamdaoensis*. *Archangiopteris*, therefore, formerly a monotypic genus, has come to comprise 4 species. As to distribution, the species are extremely local.

A. Henryi is only known from Mentzu (Yunnan); *A. Somai* exists in one or two spots in the northern part of Formosa; *A. subintegra* occurs in one place in the mountains of Chapa between Yunnan and Tonkin; and *A. tamdaoensis* is found in one locality on Mt. Tamdao (Tonkin); and the new genus is also limited to one spot on Mt. Tamdao.

Returning to the systematic position of the new genus, the most remarkable feature which separates the new type from all the other genera of the Marattiaceae is its elongated linear or even vermiform synangium. The other important characters are its horizontal dorsiventral rhizomes and simply pinnate fronds. Through the dorsiventral rhizomes it is related to *Kaulfussia* and *Archangiopteris;* by the simple pinnate fronds it is allied to *Macroglossum*, *Danaea*, and *Archangiopteris;* in the structure of the synangium its nearest of kin is to be found in *Marattia*. It is distinguishable from the latter, however, by its elongated linear synangium, simply pinnate fronds, and dorsiventral horizontal rhizome. It differs from *Archangiopteris* in having a synangium; from *Macroglossum* in the dorsiventral rhizomes and synangium; from *Angiopteris* in the simple pinnate leaves, dorsiventral rhizomes, and synangium; from *Danaea* in the synangium with a longitudinal common slit; and from *Kaulfussia* in the pinnate leaves and linear synangium. After considering all these cases, I am forced to the conclusion that the new plant must be a type representing a new genus. I propose to call it *Protomarattia*, as it bears exactly the same relation to *Marattia* as *Archangiopteris* does to *Angiopteris*.

As was stated, *Protomarattia* closely resembles *Marattia* in the reproductive organs, while it is closely related to *Archangiopteris* in its vegetative organs. The similarity of the type of the new genus and *Archangiopteris tamdaoensis* in the fronds and rhizomes, even in the serration and venation, is really so very great that I entirely failed to distinguish the one from the other until I saw the sori. The protective arrangement of stipules and commissures of our plant is exactly like that in *Archangiopteris*. The synangium also, presenting a linear form, with comparatively thinner lateral walls and a little looser connection of locules, more or less tends toward the sorus of *Archangiopteris*, or even toward that of

Macroglossum.[8] There can be no doubt, therefore, that the genus is closely related to *Marattia* on the one hand, while on the other it is nearly allied to *Archangiopteris*. It represents presumably a form of an ancient and conserved type connecting *Marattia* with *Archangiopteris*.

Protomarattia, nov. gen.—Rhizoma dorsiventrale oblique vel horizontaliter prostratum, reliquiis stipitum dense obtectum, radicibus e latere ventrali oriundis. Folia circum rhizoma spiraliter disposita; stipulis e latere adaxiali stipitis commissura connexis; stipitibus rectis duobus locis basi et superiore geniculato-incrassatis post finitas functiones e geniculo superiore et iterum basilari solutis; frondibus simpliciter pari- vel impari-pinnatis, pinnis patentibus vel interdum retrorsum reflexis; petiolulis pinnarum incrassatis. Synangium lineare submarginale e margine pinnae 4–6 mm. distans subsessile rima mediana longitudinali apertum; indusio e squamis numerosissimis laceratis inprimis constituto, demum evanescenti.

Differt a *Marattia* synangio lineari nec ovali, loculis multo numerosioribus, fronde multo minore simplicter nec pluries pinnata et rhizomate dorsiventrali repente nec erecto; differt a *Archangiopteris* synangio.

In Tonkin incola ad huc monotypica.

Protomarattia tonkinensis, sp. nov.—Rhizoma incrassatum horizontaliter vel oblique repens dorsiventrale, in specimine exsiccato nostro 15 cm. longum cum reliquiis foliorum 2.5 cm. latum, reliquiis stipitum et stipulis dense obtectum e latere ventrali radices incrassatas teretes emittens. Folia versus apicem rhizomatis 5–6 approximatim disposita. Stipites 30–40 cm. longi erecti planoconvexi in sectione duobus locis ad basin et ad 0.3 altitudinem a basi geniculato-incrassati, basi dense sursum pauce squamulati, squamulis lanceolatis vel linearibus circ. 2 mm. longis margine erosis; partibus incrassatis basilaribus geniculiformibus 2.5 cm. longis, 1.5 cm. latis utroque latere stipula et latere adaxiali commissura instructis, stipulis coriaceis tenuiter 2-lobatis, lobis abaxialibus (anterioribus) minoribus late semirotundatis, 1 cm. latis, 7 mm. longis margine erosis et membranaceis folium proprium (in

[8] CAMPBELL, D. H., The structure and affinities of *Macroglossum Alidae* Copeland. Ann. Botany **28**:664. 1914.

alabastro) obtegentibus, lobis adaxialibus (posterioribus) majoribus semi-obovatis 1.5 cm. longis 7 mm. latis margine erosis et tenuibus cum commissura alabastrum folii juxta venientis obtegentibus; partibus incrassatis superioribus geniculiformibus, 2 cm. longis, 7–10 mm. in diametro sectionis in vivo nitidis; foliis post finitas functiones ex apice partis incrassatae basilaris et e parte incrassata superiore texturae degenerationi solutis. Frondes simpliciter pari- vel impari-pinnatae in ambitu obovatae vel ovatae stipitem in longitudine fere aequantes, circ. 30 cm. longae, 20–25 cm. latae, pinnis 4–5, rarius 3–7, alternis inferioribus minoribus superioribus majoribus, patentissimis vel interdum retrorsum reflexis, pinnis superioribus lanceolatis plus minus falcatis, 25–28 cm. longis, 5–6 cm. latis apice ad caudam abrupte acuminatis (cauda apicali lineari, 2–3 cm. longa, medio 4 mm. lata, serrata), basi subito triangulari-cuneatis (parte cuneata 1.5 cm. longa latere recta integra), margine planis nec recurvis nec undulatis minute serrulatis (serrula triangulari-acuta ascendenti), supra atroviridibus nitidis subtus pallidissimis subglabris ad costam et venas paucissime squamulatis (squamula minutissima), costa utraque facie elevata 1–2 mm. lata in exsiccato nigricanti; venis parallelis a costa angulo 80° egressis simplicibus vel e basi furcatis fere rectis prope marginem subite recurvo-ascendentibus a se 1.5 mm. distantibus ad apicem serrularum attingentibus apice haud incrassatis in exsiccato nigricantibus; petiolulis pinnarum circ. 1 cm. longis incrassatis squamulatis; rhachis frondis supra medio tenuiter sulcata in vivo angustissime alata 4–7 cm. longa; textura chartacea vel chartaceo-membranacea. Synangia numerosissima subsessilia secus venas vel venulas utroque latere costae prope marginem 1-seriatim approximatimque disposita, e margine 3–5 mm. ditantia, linearia vel vermiformia 4–6 mm. longa, 1 mm. lata rima longitudinali mediana aperta, primum squamulis laceratis indusiorum obtecta demum nuda, loculis numerosissimis utroque latere receptaculi 20–60 dispositis.

HABITAT.—Monte Tamdao (Tonkin), in silva ad 3000 ped. alt., leg. *B. Hayata*, July 1917.

ARCHANGIOPTERIS Christ et Giesenhagen, Pteridographische Notizen, Flora **86**:72. 1899; BITTER, Natürliche Pflanzenfam.

1[4]:439; CHRISTENSEN, Ind. Filic. 62; CAMPBELL, Eusporangiatae, Publication no. 140, Carnegie Institution of Washington 203; LOTSY, Vorträg Bot. Stammesgeschichte 2:675.

KEY TO SPECIES

Indusium scales present between two rows of sporangia in a sorus....*A. Henryi*
Indusium scales absent between two rows of sporangia in a sorus.
  Pinnae nearly entire, scales brown.....*A. subintegra*
  Pinnae serrulate.
    Scales dark brown or blackish.....*A. tamdaoensis*
    Scales brown.....*A. Somai*

ARCHANGIOPTERIS HENRYI Christ et Giesenhagen, Pteridographische Notizen, Flora **86**:77. 1899; GWYNNE-VAUGHAN, On the anatomy of *Archangiopteris Henryi*, etc., Ann. Botany **19**:257–271. 1905.

HABITAT.—Mengtzu (Yunnan) ex HENRY.

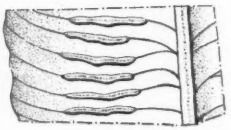


FIG. 1.—*Archangiopteris subintegra* Hayata.

Archangiopteris subintegra Hayata, sp. nov. (fig. 1).—Rhizoma horizontaliter vel plus minus oblique repens, in specimine nostro exsiccato 9 cm. longum cum reliquiis stipitum 4 cm. latum dorsiventrale reliquiis stipitum et stipulis persistentibus dense obtectum, radicibus incrassatis e latere ventrali rhizomatis oriundis. Stipes 70 cm. longus erectus basi dense sursum pauce squamulatus, squamulis lanceolatis, duobus locis basi et medio incrassatus, parte basilari incrassata 1 cm. longa totiusque lata stipulata, commissuris ut videntur obsoletis. Frons simpliciter pari- vel impari-pinnata in ambitu obovata, pinnis 5–7, superioribus majoribus lanceolatis, circ. 25 cm. longis, 5 cm. latis apice acuminatis ad caudas lineares abeuntibus (cauda 2–3 cm. longa serrulata), basi acutis margine cauda serrulata excepta fere integris; costa utraque pagine elevata, venis simplicibus vel a basi furcatis, venis et venulis parallelis a se 2.5 mm. distantibus patentissimis a costa angulo 85° egressis subrectis sursum plus minus recurvis; pagine supra nitida atroviridi, subtus pallidissima; petiolulis incrassatis 7 mm. longis squamulatis; textura membranacea. Sori lineares, 1 cm. longi, 1 mm. lati utroque latere costae 1-seriatim inter costam et marginem

dispositi a se 2.5 mm. distantes, primum squamulis filiformibus indusii obtecti demum nudi.

HABITAT.—Inter Chapa et Mueng-Xen (Tonkin), in silva ad 4000 ped. alt., leg. *B. Hayata*, July 1917.

Very distinct from the other members of the genus by the much thinner subentire pinnae.

Archangiopteris tamdaoensis Hayata, sp. nov. (fig. 2).—Rhizoma horizontaliter vel plus minus oblique repens dorsiventrale in specimine exsiccato nostro, 9 cm. longum cum reliquiis stipitum 3 cm. crassum e latere ventrali radices incrassatas teretes emittens, reliquiis stipitum et stipulis persistentibus dense obtectum. Stipes 40–45 cm. longus basi dense sursum pauce squamulatus, squamulis lanceolatis apice acuminatis vel ad acumen filiforme abeuntibus, 3–5 mm. longis, locis duobus ad basin et ad 0.3 altitudinem a basi incrassatus; parte incrassata basilari geniculiformi, 1–2 cm. longa, 1 cm. lata utroque latere stipula persistenti instructa, stipulis coriaceis latere adaxiali stipitis a commissura 2-fida connexis 2-lobatis, lobis anterioribus minoribus rotundatis 7 mm. latis totiusque longis margine erosis interiore recurvis, lobis posterioribus majoribus semi-oblongis, 2 cm. longis, 7 mm. latis margine erosis membranaceis; parte incrassata superiore stipitis geniculiformi, 2 cm. longa, 1 cm. lata; stipites post finitas functiones ex apice partis basilaris incrassatae et iterum e parte incrassata superiore texturae degenerationi soluti. Frons simpliciter pinnata in ambitu obovata pari- vel impari-pinnata, pinnis 3–4, superioribus majoribus lanceolatis, 23 cm. longis, 5.5 cm. latis apice gradatim acuminatis rarius subito acuminatis (acumine lineari 2.5 cm. longo, 2 mm. lato margine subintegro rarius serrulato), basi triangulari-acutis vel cuneatis margine praeter basin acumenque minute serrulatis (serrula triangulari-subacuta); costa utraque elevata, venis lateralibus numerosissimis parallelis patentibus a costa angulo 70° egressis subrectis simplicibus vel e basi furcatis, venulis ad apicem serrulatum attengentibus, a se 1.5 mm. distantibus; pagina supra atroviridi subnitida subtus pallidissima, supra glabra

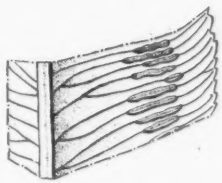


FIG. 2.—*Archangiopteris tamdaoensis* Hayata.

subtus paucissime squamulata vel glabra; petiolulis 5 mm. longis incrassatis. Sorus linearis utroque latere costae 1-seriatim secus venas vel venulas dispositus, 7–8 mm. longus, 1 mm. latus e costa circ. 1 cm. e margine circ. 4 mm. distans, primum squamulis filiformibus indusii obtectus demum nudus.

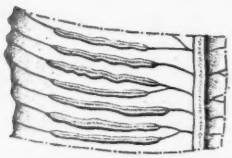


FIG. 3.—*Archangiopteris Somai* Hayata.

HABITAT.—Mt. Tamdao (Tonkin), in silva ad 3000 ped. alt., leg. *B. Hayata*, August 1917.

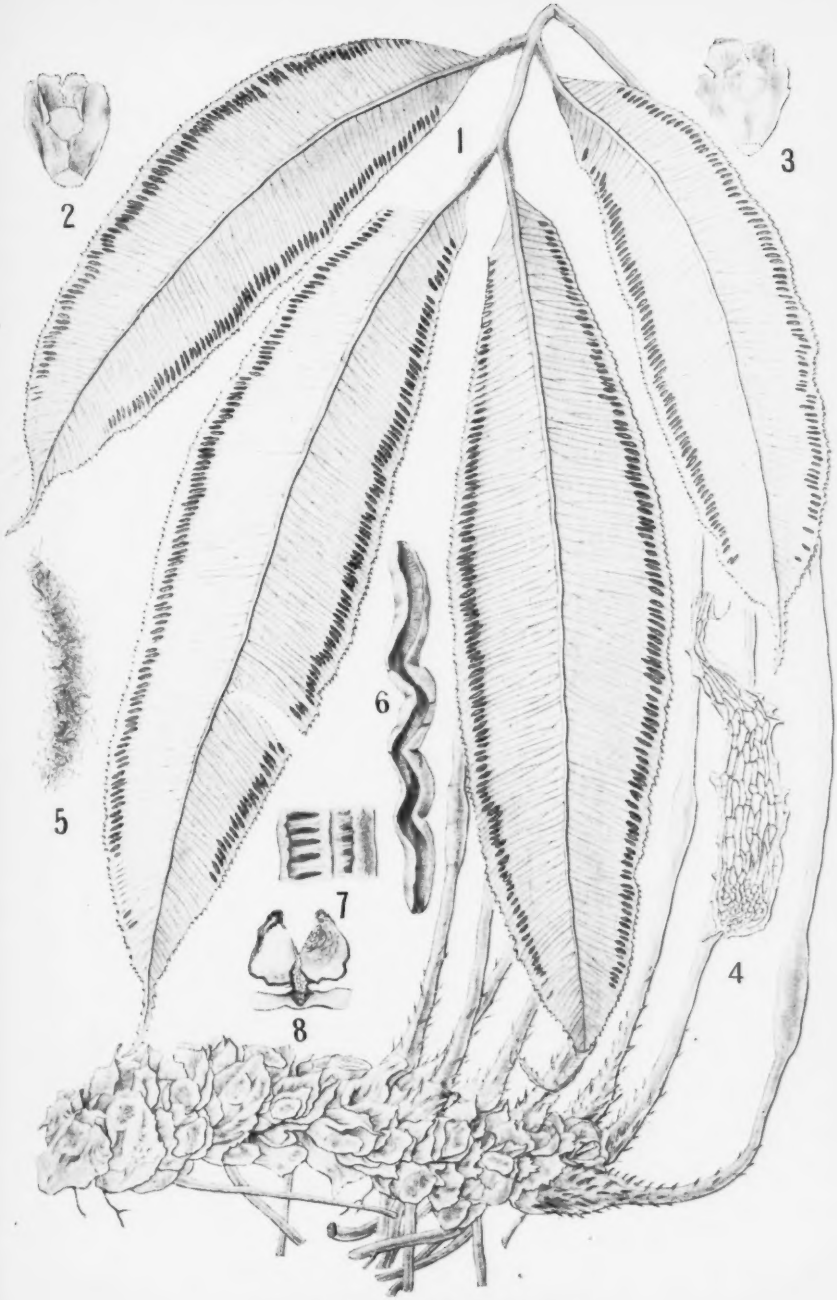
Allied to *A. Somai* Hay., but distinguishable from it in the shorter sorus located much nearer to the margin than to the costa, and in the less patent veins.

ARCHANGIOPTERIS SOMAI Hayata, Ic. Pl. Formosa 5:256; 6:154. *pl. 19* (fig. 3).

HABITAT.—Urai (Formosa).

EXPLANATION OF PLATE I

Protomarattia tonkinensis Hayata: *1*, plant; *2*, basal portion of stipe with stipules and a commissura, seen from abaxial side; *3*, same portion seen from adaxial side; *4*, scale on stipe; *5*, young synangium; *6*, full grown synangium; *7*, portion of same synangium showing chambers; *8*, section of same.



HAYATA on PROTOMARATTIA

CURRENT LITERATURE

BOOK REVIEWS

Fossil plants

The third volume of SEWARD's *Fossil plants*[1] will be welcomed alike by students of paleobotany and by those whose primary interest is in the morphology and phylogeny of the living vascular plants. The volume, comprising chapters xxvii–xxxix of the complete work, is devoted to Gymnosperms, the space being distributed as follows: Cycadales (recent) 34 pages, Pteridospermae 140, Cycadofilices 39, Cordaitales 86, Paleozoic gymnospermous seeds 66, Cycadophyta (fossil) 226, Bibliography of Vols. III and IV 48, Index 17, making a total of 656 pages. There are 252 figures, many of which are original.

The account of the living cycads, from the standpoint of a competent paleontologist, is particularly interesting and suggestive to one who, like the reviewer, is somewhat familiar with those forms, but is dependent upon investigators like SEWARD for descriptions of their extinct predecessors. This introductory chapter is a fitting introduction to the more detailed treatment of paleozoic and mesozoic members of the phylum. The practical advantage of such an introduction is sufficient excuse for treating the living cycads first instead of considering them in their natural place at the end of their phylum. The author believes the antiquity of that part of the cycadophyte phylum represented by the living cycads cannot be determined, but it is probable that if cycads, apart from Bennettitales, existed in the Jurassic and lower Cretaceous beds, they occupied a very subordinate place in comparison with the Bennettitales. While the living cycads resemble the Bennettitales in many vegetative features, we believe that the reproductive structures show a kind of difference which would make it impossible to derive the living cycads from any forms of the Cycadeoidea type; while, on the other hand, the Cycadofilicales, which SEWARD prefers to call Pteridospermae, have reproductive structures from which the cones of living cycads might easily be derived. If the living cycads have come from Bennettitales, they must have come from ancient types in which the megasporophylls still retained a distinct leaflike character. Whether they have come from the Bennettitales or directly from the Cycadofilicales, they must have greater antiquity than is indicated by any material yet discovered. We agree with SEWARD that the affinities are still in doubt, but we hope that Triassic material which can be sectioned will be found and that it will clear up relationships, for, it seems to us, the differentiation must have taken place long ago.

[1] SEWARD, A. C., Fossil plants, a textbook for students of botany and geology. Vol. III. Pteridospermae, Cycadofilices, Cordaitales, Cycadophyta. 8vo. pp. xviii+656. *figs. 253*. Cambridge University Press. 1917.

We should have treated the Pteridospermae, Cycadophyta, and Cycadales together as a cycadophyte phylum. The Cycadofilices, including fernlike plants which may belong to the Pteridospermae but in which seeds have not yet been discovered, naturally follow the known Pteridospermae; but it does not seem natural to treat the Cordaitales between the Pteridospermae and the Cycadophyta. After a careful reading of the Pteridospermae, we still fail to see why they should not be regarded as an order of the gymnosperms rather than as a group of equal rank. However, these are minor and very insignificant objections. The book is full of detailed descriptions and critical discussions which will make it possible for investigators with far less training than SEWARD to make valuable studies of such material as may fall into their hands.

The Pteridospermae are introduced by an excellent description of *Lyginopteris*, the name applied to the plant whose various fragments have been described under the names *Lyginodendron* (stem), *Sphenopteris* (leaf), *Lagenostoma* (seed), *Crossotheca* (microsporophylls), and *Kaloxylon* (root). The descriptions of *Heterangium* and *Medullosa*, while less complete, give a critical account of what is known up to date. The presentation of these 3 forms, with comparatively fragmentary accounts of others, shows where research is needed, and will enable students to fill in missing phases of life histories as material becomes available. In all the paleozoic forms of the cycadophyte phylum, information in regard to to the gametophytes and embryo, although very desirable, is very scant; but if attached seeds could be found and sectioned, the preservation seems good enough to show the desired features.

The treatment of the Bennettitales (Cycadophyta), although it occupies 226 pages, seems short in comparison with the big volumes of WIELAND. The English and French contributions to our knowledge of this group are presented in considerable detail, and the author has drawn upon WIELAND for numerous excellent figures. If well-preserved reproductive structures of the lower members of this group, especially *Williamsonia*, could be found and sectioned, the results could not fail to be important, for they would almost certainly throw light upon the origin of the living cycads.

The Cordaitales, representing the coniferophyte phylum, do not occupy so much space, but comparatively little is known about the group. If our knowledge of these forms were as complete as in case of the Bennettitales, a treatment of the Coniferales would be much simplified. As it is, the various stems, leaves, and reproductive organs referred to this group are described under their respective categories, and material is thus accumulating for a connected life history.

The chapter on paleozoic gymnospermous seeds is particularly conservative and interesting. Many morphologists would have felt little hesitation in assigning most of these seeds to one group or to another, but SEWARD, throughout the work, recognizes the danger of being too positive when dealing with unattached fragments. The characters of the various types of seeds are described and discussed. Although some knowledge of the internal structure is available, it is very evident that little is known in regard to the gametophyte. A knowledge of

the internal structure of the seeds, especially the smaller seeds, might help to connect the Cordaitales with the Pteridophytes.

The fact that the geographical distribution of plants at different stages in the development of the earth receives only disconnected treatment is excused by the plea that the space needed for Vols. III and IV (now in press) was underestimated, the original plan providing for a treatment of geographical distribution at the end of Vol. IV. However, SEWARD promises an entire volume devoted to this subject. Such a work would be welcomed by all students of morphology and phylogeny, and we hope that the volume will make its appearance at an early date.

The complete bibliography and index, together with the critical and conservative presentation of the entire subject, make the work indispensable to those engaged in research upon fossil plants.—C. J. CHAMBERLAIN.

NOTES FOR STUDENTS

Chlorophyll inheritance.—This subject seems to be a stumbling-block both for plant geneticists and cytologists. In 1913 EMERSON and EAST[2] stated that there were on record only two indisputable cases of non-Mendelian inheritance. Both of these were cases of chlorophyll inheritance. CORRENS[3] made reciprocal crosses of a variegated *Mirabilis* (*albomaculata*) with normal green plants, and discovered that in this case inheritance was strictly maternal, the pollen evidently contributing nothing. He explained this by assuming that the variegation was due to a disease of the cytoplasm which destroyed many of the chloroplasts, and that nuclei were immune to this disease. Thus the disease could be transmitted to progeny by the female parent only, since the male is supposed by cytologists to contribute only a nucleus stripped free from its cytoplasm. If one grants CORRENS' assumptions, the mechanism provided will explain this case of maternal inheritance without any violation of MENDEL'S law, for here there would be no true inheritance, but merely reinfection.

BAUR,[4] working with a *Pelargonium* which had white-margined leaves, observed an occasional pure green branch and an occasional pure white branch. Flowers on these branches when self-fertilized gave respectively pure green and pure white progeny (the latter, of course, dying in the seedling stage). A cross either way between the two branches resulted in progeny which were a mosaic of green and white. Such behavior can be accounted for by either of two explanations, but each involves a very bold assumption. If there is a Mendelian determiner responsible for the full green development, and a white

[2] EMERSON, R. A., and EAST, E. M., Inheritance of quantitative characters in maize. Bull. Agric. Exper. Sta. Nebr. no. 2. pp. 120. *figs.* 21. 1913.

[3] CORRENS, C. E., Zeitschr. Ind. Abstamm. Vererb. 2:331–340. 1909.

[4] BAUR, ERWIN, Zeitschr. Ind. Abstamm. Vererb. 1:330. 1909.

plant lacks that determiner, it would not be an unheard-of thing for a cross between the two to show a mosaic (particulate inheritance). But for pure green and pure white branches to form and breed true sexually would involve somatic segregation. Such an explanation is hard to accept, since we have been confident not only that no general reduction division ever takes place in somatic tissue, but also that segregation in individual pairs of chromosomes or parts of chromosomes is impossible elsewhere than at spore formation. We might accept such a possibility for very rare monstrosities, but the case in hand seems to be a matter of fairly regular behavior. Mutation might also account for these results, but this too could hardly be expected to take place with such regularity.

The other explanation seemed much more reasonable to BAUR, but that too he acknowledged to be unorthodox. He assumed that this was not a matter of chromosomes but of plastids, and of course somatic segregation of green and white plastids is quite reasonable. If this mechanism be the true one, however, one must also grant that plastid initials are contributed by the male parent. This last is quite unorthodox and seems flatly contradictory of CORRENS' ideas, for if enough cytoplasm is contributed by the male to introduce plastid initials, why should it not also contribute the diseased condition of CORRENS' *albomaculata?*

IKENO,[5] working on variegated races of *Capsicum*, confirms BAUR'S qualitative results, and makes the case still stronger by uncovering some very significant quantitative features. "The offspring arising from the hybridization between a variegated and a green plant in either of two reciprocal ways contain a relatively far larger number of slightly variegated (less white) plants than those arising from the self-fertilization of the same variegated plant." The intensity of variegation may be progressively diminished by repeated crosses with green plants, but not even a single self-colored green has as yet been obtained in that way. IKENO concludes that the transmission of variegation is not through the nucleus, but through the plastids in the cytoplasm; the male contributes cytoplasm and plastids.

It seems impossible to reconcile this behavior with CORRENS' maternal inheritance. To assume that plastid initials originate within the nucleus might smooth over the immediate difficulty, and would carry us into further complications. A more hopeful suggestion is that the disease which CORRENS speaks of attacks only mature chloroplasts and that plastid initials are immune, as well as the cytoplasm around them. The easiest assumption, of course, would be to claim that CORRENS overlooked a case of apogamy. Otherwise we may be driven to acknowledge that chlorophyll inheritance in angiosperms is governed by at least two mechanisms, which are not only quite different but directly contradictory.—MERLE C. COULTER.

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[5] IKENO, S., Studies on the hybrids of *Capsicum annuum*. II. On some variegated races. Jour. Genetics 6:201–229. *pl. 8. figs. 1, 2.* 1917.

Gonidia of lichens.—In 1905 ELFVING, of the University of Helsingsfors, published his studies, which he thought disproved the recent view that the chlorophyllous elements associated with lichens are algae. He continued his work and published his results in 1913. In the interval DANILOV[6] began studies which disproved ELFVING'S conclusions. DANILOV'S results were published in Russian in 1910 and in English in 1918.[7] ELFVING'S conclusion was that the lichen hyphae threw out spherical cells, at first colorless, but later colored and very similar to algae. These he supposed became separated from the hyphae and divided rapidly within the lichen thallus, forming, according to his results, the "gonidia" of lichens. Reviewing these results, DANILOV found on careful study that unstained preparations often left the impression that the algal cells might really be outgrowths of the lichen hyphae, with which they are intimately associated. By the use of stains, however, he was able to trace the entrance of the hyphae into the algal cells, thus proving that there is no genetic relationship, but that the relationship is rather that of host and parasite. The "pale gonidia" of ELFVING were found to be dead algae which had been killed by the parasitic lichen, and DANILOV was able to see distinctly the lichen hyphae within them.

Important and quite apart from the refutation of the once generally accepted view of the origin of the chlorophyllous "gonidia" from the non-chlorophyllous lichens, are the conclusions of DANILOV regarding the relation of the lichen to its algal host. He admits that there may be osmotic filtration of certain materials from the alga to the lichen, and the like passage of others from the lichen to the alga. However this may be, DANILOV finds the final result to be the absorption of the algae by the lichen hyphae, which enter the algal cells and form dense networks of slender, thin-walled or naked absorbing threads. Although the lichen thallus with its prepared peptones and certain other organic materials is probably a favorable substratum for the algae, yet the lichen is parasitic on the algae, which are killed in large numbers as a result of the parasitism. On the whole the algae thrive better outside the association with the lichen, while the lichen does poorly or dies outright outside the association.—BRUCE FINK.

Sex organs of Phytophthora.—In 1913 PETHYBRIDGE,[8] studying a disease of the potato produced by a phycomycetous fungus which he named *Phytophthora erythroseptica*, observed that on the formation of the sexual organs of this

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[6] DANILOV, A. N., Über das gegenseitige Verhältnis zwischen den Gonidien und dem Pilzkomponten der Flechtensymbiose. Bull. Jard. Imp. Bot. St. Petersb. **10**:33–70. *pls. 3. figs. 9.* 1910.

[7] ———, The relation between the gonidia and the hyphae in lichens. Jour. Botany **56**:169–181. 1918.

[8] PETHYBRIDGE, G. H., On the rotting of potato tubers by a new species of *Phytophthora* having a method of sexual reproduction hitherto undescribed. Sci. Proc. Royal Dublin Soc. **13**:529–565. *pls. 3.* 1913.

fungus the oogonial hypha pushes its way entirely through the antheridium, and, after emerging on the side opposite to the point of entrance, enlarges to form the oogonium. This unusual process, together with the subsequent events in the formation of the oospore, has now been more fully investigated by MURPHY,[9] whose cytological evidence bears out the observations of PETHYBRIDGE. The antheridia and oogonia are found to arise on different branches of the mycelium. During the penetration of the antheridium by the oogonial incept no fusion of the cytoplasm of the two organs occurs. After its emergence the oogonial hypha develops into a more or less spherical multinucleate oogonium whose stalk passes through the antheridium. When the sexual organs have reached their full size, about two-thirds of the nuclei in the antheridium and in the oogonium degenerate. The remaining nuclei in both organs then divide once mitotically and simultaneously. During the division the nuclei of the oogonium are arranged in a hollow sphere, with the exception of one, which remains in the center. Immediately after the division the protoplasm of the oogonium separates into a vacuolate hyaline ooplasm and a denser periplasm. In the oogonium, and probably in the antheridium also, all the nuclei but one degenerate. During this period a prominent receptive papilla protrudes from the base of the oogonium into the antheridium. When the receptive papilla is withdrawn, the fertilization tube grows into the oogonium at the same point and discharges one nucleus and the greater part of the cytoplasm of the antheridium into the oogonium. With the completion of this process most of the periplasm has disappeared and the oospore is surrounded by a thin membrane with the last vestiges of the degenerating nuclei appressed against its outer surface. The fusion of the two nuclei does not take place until the thickened oospore wall has been completed.—H. HASSELBRING.

Action of neutral salts on acid inversion of cane sugar.—LEBERT[10] has studied the action of neutral salts on the acid inversion of cane sugar. His results furnish him a basis for a chemical explanation of certain difficulties sometimes encountered when attempts are made to invert cane sugar by means of weak acids or stronger acids in quantity just sufficient to effect the inversion. Solutions in which it is desired to invert cane sugar are rarely free from neutral salts, especially sodium acetate left in the solution after clearing with lead acetate and removing the excess of lead with sodium carbonate or sulphate. If the hydrolysis is effected by a relatively large quantity of strong acid, as in the Clerget method, the presence of a small amount of salt is of little consequence, since the H ions are in great excess. If organic acids are employed, the presence of their sodium or potassium salts will retard the rate of inversion,

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[9] MURPHY, P. A., The morphology and cytology of the sexual organs of *Phytophthora erythroseptica* Pethyb. Ann. Botany **32**:115–153. *pls.* 3. 1918.

[10] LEBERT, M., Action des sels neutres sur l'inversion du sucre par les acides. Rev. Gen. Botanique **30**:241–244. 1918.

the decrease in the rate depending upon the strength of the acid; the weaker the the acid the greater the inhibiting action of its salt. The action of acetic acid is completely paralyzed by the presence of sodium acetate equivalent to the proportion of the acid. The effect of a salt other than the salt of the acid used for the inversion depends upon the relations established between the acid and the salt. An example would be HCl in the presence of sodium acetate; NaCl and acetic acid are formed. If the acetate is present in sufficient quantity, all of the HCl is replaced by acetic acid, and if the acetate is still in excess, we have inversion by acetic acid in the presence of its sodium salt, in which case the hydrolysis is always inhibited. The author offers a similar explanation for a situation reported by DAVIS and DAISH. They found that 2 per cent citric acid was sufficient to invert a solution of cane sugar by boiling 10 minutes, but it was without effect in the presence of a certain quantity of sodium acetate. The citric acid reacted with the sodium acetate, giving sodium citrate and liberating an equivalent amount of acetic acid, the action of which was paralyzed by its sodium salt still present in the solution.—CHARLES O. APPLEMAN.

Effect of different oxygen pressures on carbohydrate metabolism of sweet potatoes.—The experiments reported by HASSELBRING[11] in this paper were designed primarily to effect a further separation of the various steps in the transformation of starch to sugar in sweet potatoes. For this purpose different oxygen pressures were employed. When the sweet potatoes are killed under a gas pressure of 5 atmospheres, starch hydrolysis is greatly depressed or inhibited. In the living potatoes starch hydrolysis and cane sugar formation proceeded in the absence of oxygen in the same manner as in air or in an atmosphere of oxygen. CRUICKSHANK working with barley seed, and BOYSEN-JENSEN working with germinating barley and peas, found that cane sugar was not formed in the absence of oxygen. These investigators conclude that the presence of oxygen is one of the necessary conditions for cane sugar formation, but since this was not found to be the case with sweet potatoes, the conclusion is not of general applicability.

Anaërobic respiration in sweet potatoes consumes, in a given period of time, a greater quantity of material than is consumed by normal respiration. The energy derived from a given mass of material is less in anaërobic than in normal respiration. These facts, coupled with the observation that cane sugar is formed with equal facility under anaërobic and aërobic conditions, lead the author to believe that his experiments in a general way support the BOYSEN-JENSEN theory that the respiratory processes furnish the energy for the synthesis of cane sugar. In the case of the sweet potato this energy could be furnished by anaërobic respiration.

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[11] HASSELBRING, HEINRICH, Effect of different oxygen pressures on the carbohydrate metabolism of the sweet potato. Jour. Agric. Research **14**:273–284. 1918.

Another very interesting fact brought out by the author's work on sweet potatoes is the apparent stability of cane sugar in relation to the respiratory processes in these roots, as cane sugar does not seem to be consumed by either anaërobic or normal respiration.—CHARLES O. APPLEMAN.

Analysis of quantitative variation.—BROTHERTON and BARTLETT[12] have presented the results of a very significant piece of research. The investigation as it stands belongs to the field of plant physiology, but probably it is most significant in the bearing upon certain problems of genetics. Plants of *Phaseolus multiflorus* grown in light and darkness were compared as to length and number of epidermal cells of a given internode. For the physiologist the results may be summarized in the following statement: "The effect of light is that it retards extension of the cells, and that as an indirect result there are fewer secondary divisions, since relatively fewer primary cells enter the range of length within which division takes place." For the geneticist we quote the following: "The mathematical formulation of the results of size inheritance according to the multiple factor hypothesis should be paralleled by a biological analysis, the object of which is the identification of the several factors concerned." Thus size differences may be resolved into number or size of constituent cells or both. "In the investigation of quantitative variations of a hereditary nature it seems likely that the study by the histological method of reactions to the environment and of the obscure reaction known as 'vigor of heterozygosis' will afford a means of correcting for these disturbing factors." It is probably true that heritable size differences express themselves directly in the cells of tissues deeper than the epidermis, and that the change in the epidermis amounts merely to a mechanical response to these forces within. It would probably be advisable, therefore, to carry the analysis to more significant tissues.—MERLE C. COULTER.

Root growth in cuttings.—CURTIS[13] has published an important contribution to the physiology of root formation in cuttings. A number of forms were used, but *Ligustrum ovalifolium* furnished most of the experimental material. Nutrient solutions of the strengths used in culture work with seedlings were found to be distinctly injurious to woody cuttings. Treatments with potassium permanganate resulted in a very marked increase in root growth of various woody cuttings. After discussing several possible explanations for this stimulation, the author concludes that it is most probable that the potassium permanganate increases respiratory activity by catalytically hastening oxidation. It is known that when potassium permanganate comes in contact with organic matter manganese dioxide is precipitated and oxygen is liberated. There was

[12] BROTHERTON, WILBER, and BARTLETT, H. H., Cell measurement as an aid in the analysis of quantitative variation. Amer. Jour. Bot. 5:192–206. 1918.

[13] CURTIS, OTIS F., Stimulation of root growth in cuttings by treatment with chemical compounds. Cornell Univ. Agric. Exper. Sta. Memoir 14:71–138. 1918.

some indication that other inorganic compounds may stimulate root growth in cuttings. The author's work gives further strong evidence that callus and root growth is independent of the rest period and that only the buds assume the resting condition. Immature twigs were caused to absorb cane sugar which increased root development. Mature twigs, however, were but slightly benefited. When the base of cuttings were placed in sugar solution for a short time, the terminal bud of the twig failed to develop in a normal manner and the lower buds formed shoots instead. The author believes that many of the practices commonly followed by greenhouse and nursery men in the propagation of plants by cuttings are explainable on the basis of better aëration. The discussions of the literature are comprehensive and critical.—CHARLES O. APPLEMAN.

Vegetation of Newfoundland.—In contrasting the divergent floras of different parts of Newfoundland, FERNALD[14] bases his explanation of their differences upon the hypothesis that "the presence or absence of varying degrees of available lime or of other bases in the soil is more fundamental in determining plant distribution than are even considerable differences of temperature and humidity."

The calcareous and at the same time the most fertile portion of the island is along the west shore, where the ordinary observer would be surprised to find the indigenous flora of the warmest and most fertile region of the island composed very largely of species of high northern distribution, such as *Juncus triglumis*, *Saxifraga oppositifolia*, *S. aizoides*, *S. caespitosa*, *Salix vestita*, *Dryas integrifolia*, and *Lesquerella arctica*. These FERNALD explains as being from the calcareous habitats of the arctic archipelago and the Canadian Rockies, the lime being hostile to the plants of the siliceous adjacent mainland. The eastern part of the island, the central tundra district, and the southwest corner, in spite of the fact that they are cold, bleak, and barren, are populated mainly by plants of the southern Atlantic coast region, with an addition of some like *Calluna vulgaris* and *Pedicularis sylvatica* from the acid soils of western Europe.

Maps of the distribution of a dozen species give graphic demonstration of the remarkable distribution of some of the more important plants and serve to make the evidence in the support of his hypothesis the more convincing.—GEO. D. FULLER.

Physiological rôle of glucosides in plants.—Continuing his investigations on the physiological rôle of glucosides in plants, COMBES[15] has made the interesting discovery that a given glucoside is not toxic to a plant which naturally

[14] FERNALD, M. L., The contrast in the floras of eastern and western Newfoundland. Amer. Jour. Bot. **5**:237–247. *pls. 3.* 1918.

[15] COMBES, RAOUL, Recherches biochemiques experimentales sur le rôle physiologique des glucosides ches les vegetaux. Rev. Gen. Botanique **30**:226–237, 245–257. 1918.

produces it, but is very toxic to plants belonging to a species in which the glucoside is not naturally found. The toxic glucoside, when added to Knop's culture medium in which the plants are grown, produces very marked abnormal changes in the morphology of the roots, resulting also in a very stunted growth of tops. It appears that we have here another group of substances, the individuals of which possess a constitution sufficiently characteristic of the species in which they are found that when they are applied to individuals belonging to nonrelated species they produce abnormal responses. The author has not yet found that glucosides will furnish carbohydrate food for plants when they are grown in a carbon dioxide free atmosphere, as has frequently been found to be the case with glucose.

Those wishing to germinate seeds and grow seedlings under aseptic conditions will be interested in the detailed descriptions of the apparatus and procedures employed in growing his plants. An excellent review of the mass of literature on the subject and a survey of glucosides in plants will be found in the earlier papers of this series.—CHARLES O. APPLEMAN.

Physiology of fungi.—DUGGAR, SEVERY, and SCHMITZ[16] have undertaken a study of the comparative nutrient value of some of the decoctions ordinarily used in the preparation of culture media for fungi. The decoctions which were prepared on the basis of 50 gm. of dry matter to a liter of water were made from bean, sugar beet, prune, potato, turnip, cornmeal, apple, mangold, celery, carrot, and salmon. The standard decoctions were employed alone and in combination with sugar and various mineral nutrients. It was found that in their nutrient value the decoctions are very dissimilar for different fungi. The addition of sugar in most cases increases the yield, but the addition of sugar with nitrate and phosphate gives a very much greater yield than the addition of any of these substances alone. It is pointed out also that the standardization of the decoctions on Fuller's scale leaves them differing widely in hydrogen ion concentration. This work brings out the fact that little is really known of the nutrient value of plant decoctions, which it appears are generally deficient in nutrients and require the addition of considerable "fertilizer" to produce the greatest growth of fungi.—H. HASSELBRING.

Maps of rainfall and crop plants.—Among the recent publications of the United States Department of Agriculture there are two at least of decided interest to ecologists and plant geographers. The first is a rainfall map of the United States[17] embodying the data from not less than 3600 stations. The precipitation is given in inches and the map is in 8 shades of blue. An interesting insert map gives the rainfall from April 1 to September 30, and exhibits a

[16] DUGGAR, B. M., SEVERY, J. W., and SCHMITZ, H., Studies in the physiology of fungi. Ann. Mo. Bot. Gard. **4**:165–173; 279–288. 1917.

[17] KINCER, JOSEPH B., Atlas of American agriculture. Advance sheet **1**: Precipitation. U.S. Dept. Agric. Weather Bur. 1917.

close relationship between the maximum summer rainfall and the grasslands of the country.

The second publication[18] contains relief and precipitation maps of the world and numerous larger and smaller maps showing the agricultural production of all lands. Many other data are contained in the text and in various tables. Several recent papers have successfully related crop possibilities to natural vegetation, but these maps provide material for reversing the process and of relating natural vegetation to areas of crop production.—GEO. D. FULLER.

Seedling of dicotyledons.—SINNOTT[19] has made a comparative study of the seedling throughout dicotyledons, in order to distinguish between conservative and variable characters. It is a very timely distinction to emphasize, for the application of the law of recapitulation to variable characters has led to more or less confusion. The number of protoxylem poles is found to be a very variable character. More constant is the relation between the vascular system of the hypocotyl and that of the epicotyl, two main types being recognized. The venation of the cotyledon was found to be very constant; and also an odd number of veins was found to characterize the seedling of all dicotyledons, distinguishing it from that of the gymnosperms. The most conservative character is the structure of the cotyledonary trace.—J. M. C.

Monographs on experimental biology.—The first volume of a series of monographs dealing with experimental biology and general physiology has appeared under the editorship of JACQUES LOEB, T. H. MORGAN, and W. J. V. OSTERHOUT. The first monograph[20] deals with forced movements, tropisms, and animal conduct. Among the monographs in preparation are "The chromosome theory of heredity" by T. H. MORGAN; "Inbreeding and outbreeding; their genetic and sociological significance," by E. M. EAST and D. F. JONES; "Pure line inheritance," by H. S. JENNINGS; "The experimental modification of the process of inheritance," by R. PEARL.

This series represents an important event in American science, and deserves the cooperation of the scientific men of the country.—J. M. C.

A new phytopathological journal.—The first number of the *Annals of the Phytopathological Society of Japan* has just appeared, including 5 papers. Some of the papers are in English, and those in Japanese include a summary in English, so that all of them are available for foreign botanists. The contributors to this first number and their titles are as follows: M. SHIRAI, "On the

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[18] FINCH, V. C., and BAKER, O. E., Geography of the world's agriculture. 10× 13.5 inches. pp. 149. *figs. 207*. 1917.

[19] SINNOTT, E. W., Conservatism and variability in the seedling of dicotyledons. Amer. Jour. Bot. 5:120–130. *figs. 4*. 1918.

[20] LOEB, JACQUES, Forced movements, tropisms, and animal conduct. 8vo. pp. 209. *figs. 42*. Philadelphia: J. B. Lippincott Co. 1918. $2.50.

development of plant pathology in Japan"; S. ITO, "A preliminary report on a late blight resistant strain of potato"; T. HEMMI, "Vorlaüfige Mitteilung über eine neue Anthraknose von *Evonymus japonica*"; S. MIURA, "On the grain of barley or wheat, infected by smut fungus through the flower"; S. HORI and U. BOKURA, "Soy bean cake as a substitute for peptone in the preparation of nutrient media."—J. M. C.

Evolution of maize.—WEATHERWAX[21] has made a detailed study of the origin of maize, concerning which there has been much discussion. A comparative study of many varieties of maize and related species has led him to the theory that vestigial organs indicate that *Zea*, *Euchlaena*, and *Tripsacum* are of the same structural type, their present peculiarities being due to the suppression of parts present in a primitive ancestor with perfect flowers and one type of inflorescence. The ear of maize is regarded as the homologue of the central spike of the tassel. The prevailing theory that maize is of hybrid origin he regards as untenable, his conclusion being that *Zea* and the other two genera mentioned "have descended independently from a common ancestral form now extinct."—J. M. C.

Ferns of Borneo.—COPELAND[22] has brought together in a convenient list the ferns of Borneo, accompanied by analytical keys. The fern flora is very impressive, including 697 recorded species, representing 88 genera. In another paper[23] the same author shows that the riches of the fern flora are far from exhausted, for he describes 43 new species from Borneo, 12 of which are species of *Cyathea*, and also a new genus (*Oreogrammatis*) related to *Polypodium*.—J. M. C.

Bryophytes of Iceland.—HESSELBO[24] has published a rather complete account of the Bryophytes of the island of Iceland. His annotated list shows 93 species of the Hepaticae, 20 of the Sphagnales, and 325 of the Musci. These he further discusses as to their aggregation in communities and their altitudinal and horizontal distribution.—GEO. D. FULLER.

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[21] WEATHERWAX, PAUL, The evolution of maize. Bull. Torr. Bot. Club **45**:309–342. *figs. 36.* 1918.

[22] COPELAND, E. B., Keys to the ferns of Borneo. Sarawak Mus. Journ. **2**:287–424. 1917.

[23] ———, New species and a new genus of Borneo ferns. Philipp. Jour. Sci. **12**: 45–65. 1917.

[24] HESSELBO, AUG., The Bryophyta of Iceland. The Botany of Iceland. Ed. by ROSENVINGE, L. K., and WARMING, EUG. **1**: pt. II. 397–676. 1918.